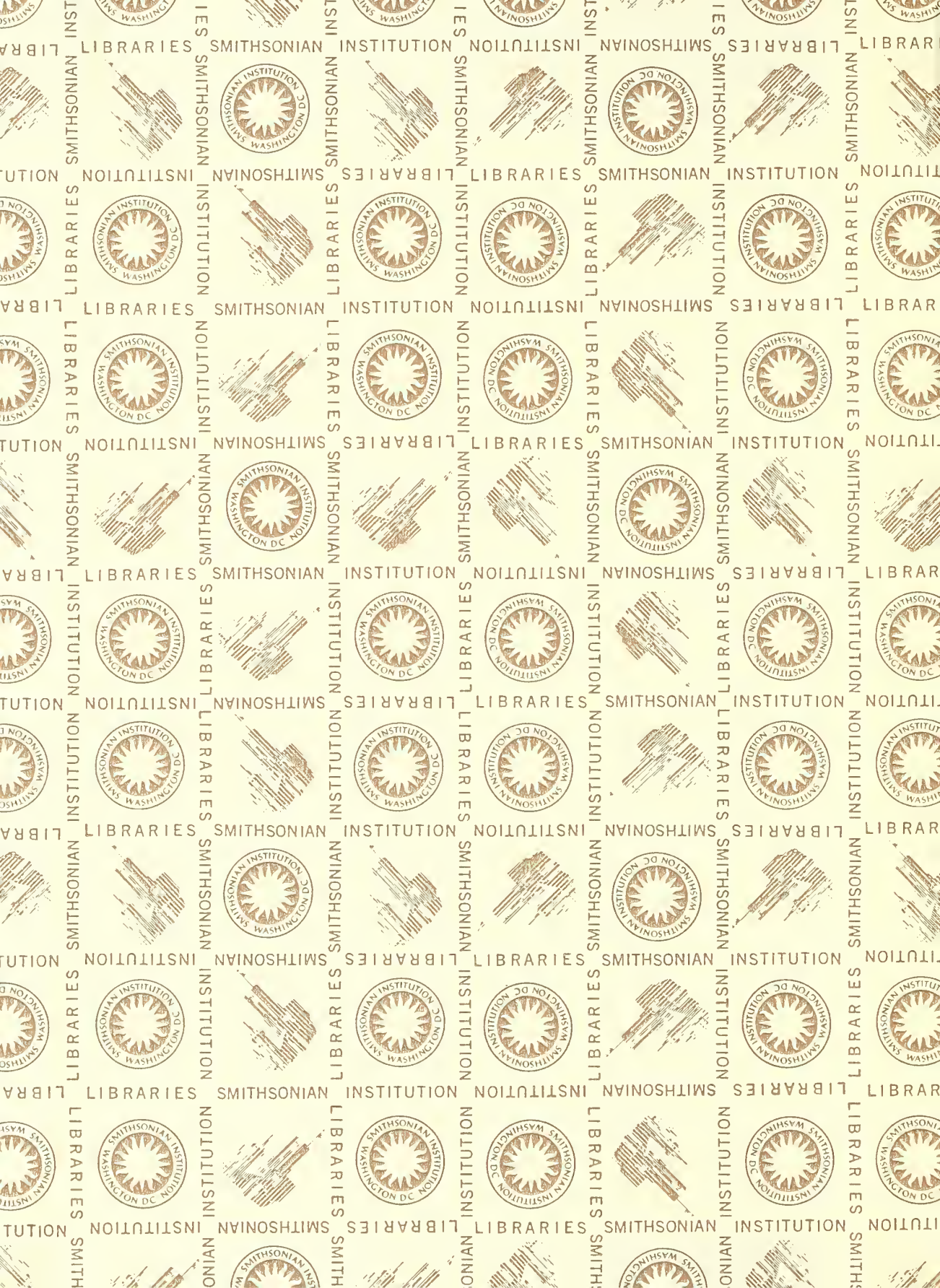






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Cover: A Middle Jurassic megaspore, *Minerisporites richardsoni* (Murray) Potonié, from Oxfordshire (× 350, S.E.M. by T. M. Windle).

STRUCTURE AND INCREMENTAL GROWTH IN THE AHERMATYPIC CORAL *DESMOPHYLLUM CRISTAGALLI* FROM THE NORTH ATLANTIC

by J. E. SORAUF and JOHN S. JELL

ABSTRACT. *Desmophyllum cristagalli* has some characteristics in common with other ahermatypic corals living in deep water (2000 m for our specimens). This weakly colonial species is characterized by a theca greatly thickened by deposition of stereome, also forming massive deposits within the corallite and sometimes completely filling it. Septal trabeculae are uniformly small in diameter in this species, and tend to blend into a fine-grained septal 'dark line' when seen in transverse thin section. These characteristics are seen elsewhere in the family Caryophylliidae and also are noted in some other deep-water-dwelling ahermatypic corals. Incremental, perhaps periodic, growth of exoskeleton is noted in these specimens of *D. cristagalli*, although they originated in a deep, apparently stable environment.

BASIC microstructural and architectural features of the ubiquitous deep-water ahermatypic coral *Desmophyllum cristagalli* Milne Edwards and Haime, 1848, are similar but not identical to those described for shallow-water hermatypic corals (Sorauf 1970, 1972; Wise 1970; Jell 1974; Jell and Hill 1974). Even in their dark and cold-water environment, these corals exhibit incremental growth which may be periodic. Structural details of this species, together with data on ahermatypic corals from the families Caryophylliidae, Flabellidae, and Dendrophyllidae (Sorauf 1970; Sorauf and Podoff, in press), should eventually be of aid in interpreting fossil corals and their palaeoenvironments. These details are also judged of interest for the understanding of the mode of calcification in scleractinian corals and especially in determining the effect of algal symbionts (zooxanthellae) which are apparently of great importance in the calcification processes of reef-dwelling corals.

This study included optical and scanning electron microscopy of the microstructure of specimens of *D. cristagalli* from a depth of 2000 m in the North Atlantic Ocean. This structure has been ascertained from study of external surfaces, broken transverse and longitudinal sections, thin sections, and polished and etched sections. This allows consideration of the mode of formation of theca and the lateral thickening of the septa by stereome, sometimes with the resultant total filling of the interseptal spaces, and also allows speculation on incremental growth of skeletal elements.

MATERIAL AND METHODS

Specimens of *D. cristagalli* were kindly made available for this study by Dr. J. R. Cann, Department of Environmental Sciences, University of East Anglia, Norwich, England. They are fresh-appearing specimens dredged from 2000 m at latitude 36° 34' N., longitude 11° 46' W. in the North Atlantic Ocean (Station 056 of the *Shackleton* 1972 cruise). The material has been deposited in the British Museum

(Natural History), London, and catalogue numbers refer to the coral register of the Palaeontology Department.

Material for scanning electron microscopy was prepared in a manner similar to that outlined by Sorauf (1972). Scanning electron microscopy was done on the AMR model 900 S.E.M. in the Department of Geological Sciences, State University of New York at Binghamton, and on the Cambridge Stereoscan S.E.M. model 1a, housed and operated by the University of Queensland Electron Microscope Centre, Brisbane.

Genus DESMOPHYLLUM Ehrenberg, 1836

Type species. *D. cristagalli* Milne Edwards and Haime, 1848, Holocene, from off Cape Breton.

The genus includes sessile, essentially solitary, trochoid forms, although loosely colonial forms consisting of many corallites budding irregularly are known (Squires 1959, figs. 8, 10). The corallites are usually taller than wide, flaring upwards from a narrow cylindrical base and often fixed to the substrate by lateral cementation of the proximal parts. The septa are numerous, closely spaced, exsert, and extend to the axis. The genus is marked by a somewhat thick, dense wall composed largely of stereome; no epitheca is distinguishable. Costae are well developed near the calice but are obsolete and covered by stereome elsewhere in most species. Sparse endothecal dissepiments are developed in some of our specimens. Columella and pali are absent.

Desmophyllum is the nominate genus of an entirely ahermatypic subfamily of the family Caryophylliidae, itself largely composed of ahermatypic genera. The genus is widely distributed in all major oceans and in water as deep as 2000 m, with a fossil record dating back to the Middle Cretaceous (Wells 1956, p. F426).

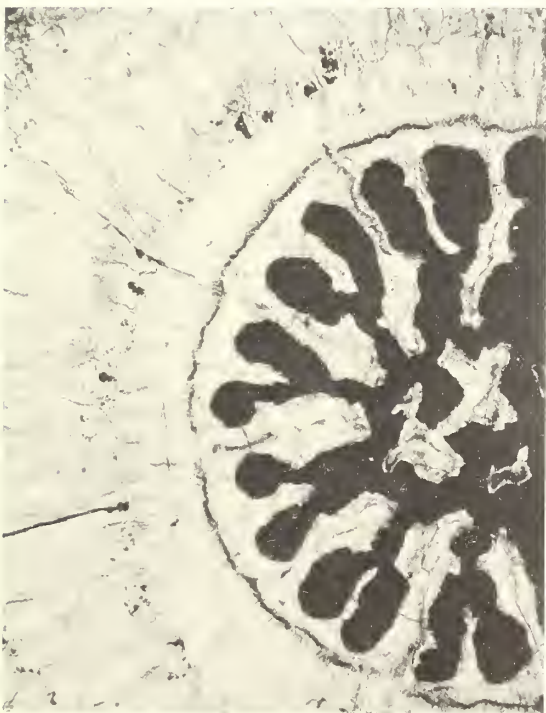
Desmophyllum cristagalli Milne Edwards and Haime, 1848, p. 253

D. cristagalli is at present broadly interpreted, allowing a large amount of variation in this cosmopolitan coral. The microstructure of this species, or of any other species of *Desmophyllum*, has not been established previously.

Description of material. The two specimens studied are both broken basally so that the attachments are missing (Pl. 1, figs. 1-3); they are 35 and 40 mm in height with

EXPLANATION OF PLATE I

Figs. 1-6. *Desmophyllum cristagalli*, Recent, Atlantic Ocean. 1, transverse calicinal view of single corallite illustrating exsert septa (BMNH 1975.10.20.1), $\times 2$. 2, longitudinal view of budded specimen to show costal ridges in the calicinal part of the individual and the granulose surface of the thick theca (BMNH 1975.10.20.2), $\times 2$. 3, calicinal view of specimen in fig. 2 illustrating small individuals of *Trochocyathus* on skeleton. Note that sample has been rotated so that broken bud at base is that seen in fig. 2 (BMNH 1975.10.20.2), $\times 2$. 4, photomicrograph of transverse thin section through exsert septa at calicinal margin showing central dark lines in septa and crystal orientation approaching perpendicularity to septal flanks (BMNH 1975.10.20.3), crossed nicols, $\times 25$. 5, transverse thin section through immature portion of corallite with development of thick stereome on outside of small diameter corallite (BMNH 1975.10.20.3), crossed nicols, $\times 25$. 6, transverse thin section through older portion of corallite with biogenic aragonite filling interseptal spaces to form solid massive cross-section (BMNH 1975.10.20.3), crossed nicols, $\times 25$.



calical diameters of 18–25 mm and 19–25 mm respectively. Corallites are trochoid, flaring distally from slightly curved tubular bases (5–7 mm diameter) with the calices crowned by a series of prominent exsert septa. The walls of the basal parts of the corallites are thick and dense; the surface here is even but finely granulose whereas the upper 20 mm shows twelve well-developed costal ridges with the most prominent corresponding to the first cycle of septa (Pl. 1, figs. 1, 2). Both specimens show the basal attachments of juvenile corallites arising from these corallites.

Both specimens show the loosely colonial corallum (Pl. 1, figs. 2, 3). Some juveniles have developed by budding off from the parent while others have developed from planulae settling on an abandoned part of the corallum. The latter is most certainly the case for the small *Trochocyathus* individual seen at the left edge of fig. 3 on Plate 1. The coralla are coated with a fine layer of manganese oxide and the outer margin is deeply bored.

Septa in four cycles with nearly complete insertion of the fifth cycle, reach to the axis. Below the calice they are fine, flexuose, relatively smooth with occasional granulations and meet at the axis. They may be geniculate axially. In the calice, the septa thicken, especially over the calicinal rim where the exsert septa are smooth and rounded. They descend steeply to the calical floor with their free axial portions showing prominent growth lines paralleling the proximal edge with regularly developed granulations likewise present on septal flanks.

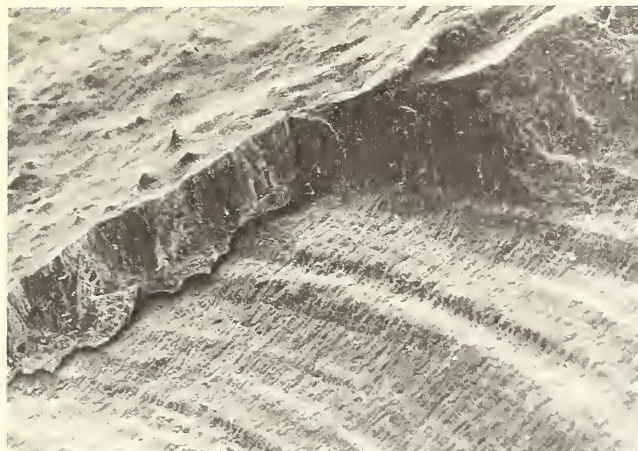
Endothecal dissepiments are irregularly developed at varying levels with the first encountered immediately below the calice.

MICROSTRUCTURE

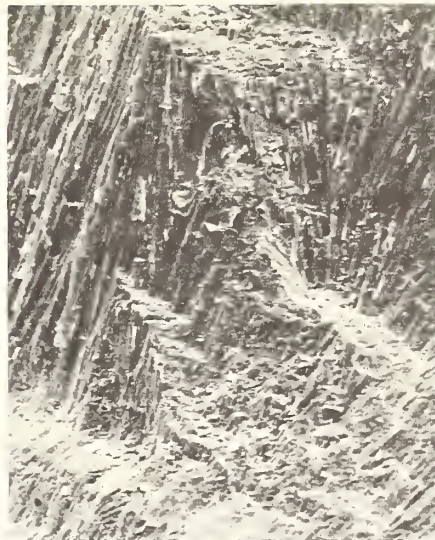
Septal structure. The septa of *D. cristagalli* have a tendency to break along a central zone within the septum (axial 'plane' of the septum), with the resultant exposure of this surface as seen in the scanning electron micrograph forming fig. 1 of Plate 2. Broken interfering clusters of aragonite crystallites (Pl. 2, fig. 2) are noted forming lateral additions to the axial zone. This thickening layer has crystallite clusters showing true physical interference with the growth of neighbouring clusters to form the septal flank material as noted here. This is somewhat different from septal flanks seen in many modern corals in that we note here a tendency for clusters to continue growth as somewhat coherent units, instead of forming crystallites oriented more

EXPLANATION OF PLATE 2

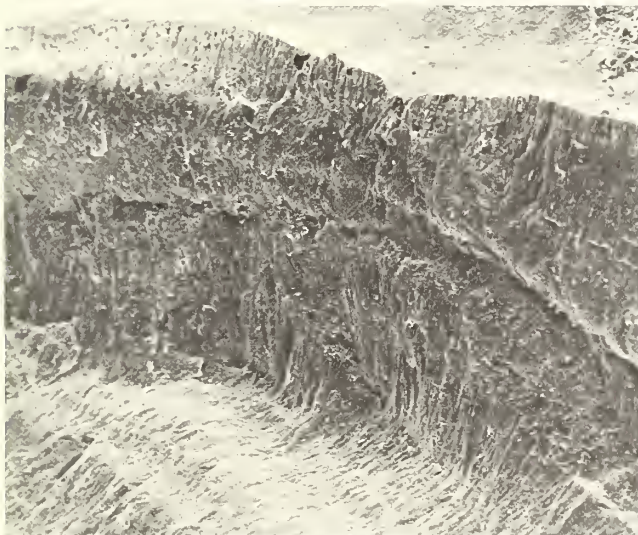
Figs. 1–6. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, septum broken along axial plane with resultant wrinkled surface, gently curved crystals bending out from axial plane to form palisade at upper right, and crystal growth in interfering clusters which thicken septa, $\times 50$. 2, enlargement of upper-right portion of fig. 1 showing bending crystal clusters and divergence of crystals within cluster, $\times 200$. 3, axial surface with crystals bending out from central zone to thicken septum, and with a prominent plane of discontinuity within the palisade where one cluster of crystallites overgrows another, $\times 100$. 4, view of broken surface of axial 'plane' of septum with apparent wrinkles, $\times 200$. 5, broken crystallite clusters from 'growth wrinkle' shown in fig. 4, illustrating how crystal cluster growth deviates from axial plane, $\times 1000$. 6, enlargement of another broken crystallite cluster showing tufting of crystallites along ridges, $\times 2000$.



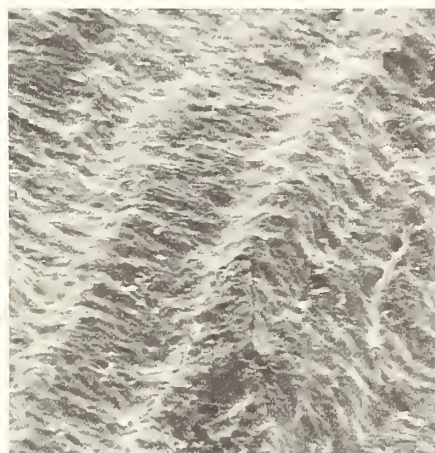
1



2



3



4



5



6

or less parallel to one another and perpendicular to the outer surface of the skeletal element. It should here also be noted that *Desmophyllum*, unlike other corals studied in detail (to date), has a very different aspect in sections broken parallel to the axial zone of the septum (as in Pl. 2, fig. 2), and sections broken perpendicular to the long axis, along incremental growth lines (Pl. 2, figs. 1, 3). In the latter case, crystallites are close to parallel as they bend out from a growth 'ridge', contrasting with the interfering clusters noted previously in sections with the orientation parallel to the axial zone (Pl. 2, fig. 2). The relationship between crystallite growth clusters, each cluster expanding rapidly, is a relationship of competition for space and mutual interference. There are definite victorious clusters in each interfering pair, with resultant overgrowth. One such line of overgrowth is shown in fig. 3 of Plate 2.

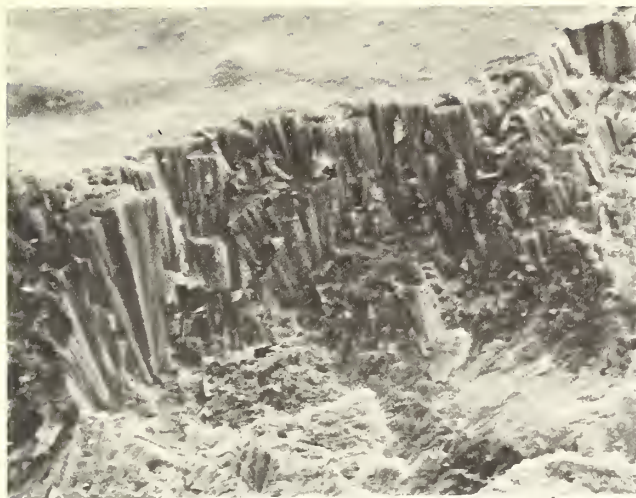
The broken surface of the axial region of the septum is wrinkled (Pl. 2, fig. 4) by ridges formed by broken crystallite clusters which diverge from the axial plane of the septum (Pl. 2, fig. 5). Upon close inspection, one notes broken tufts of crystallites (Pl. 2, fig. 6) where calcification has apparently been rapid and crystals diverging greatly. These clusters then form the palisaded thickening of the septa (Pl. 3, fig. 1). Within individual clusters (Pl. 3, fig. 2) a difference in perfection of crystallites is noted, with sub-rounded crystal forms common at the apex and broad, dense, large crystallites forming further out from the apex (Pl. 3, figs. 2, 3). The latter are most likely compound, but fracture as single crystal units.

Thin sections transverse to septa near the calicinal rim show the development of lateral crystallites approximately perpendicular to the flank surface of the septum, and diverging from a thin central row of very fine trabeculae (Pl. 1, fig. 4), which appears as a 'central dark line' in low-power photomicrographs (Pl. 1, fig. 4). The laterally contiguous trabeculae are of small diameter and composed of extremely fine crystallites (Pl. 3, figs. 4, 5). At these higher magnifications, it is also clear that the outer flanks of the septa are formed by mutually interfering radiating clusters of crystals, here with growth lines etched into prominence (Pl. 3, figs. 4, 5). In these last figures, the surprisingly cohesive nature of the clusters is also well shown.

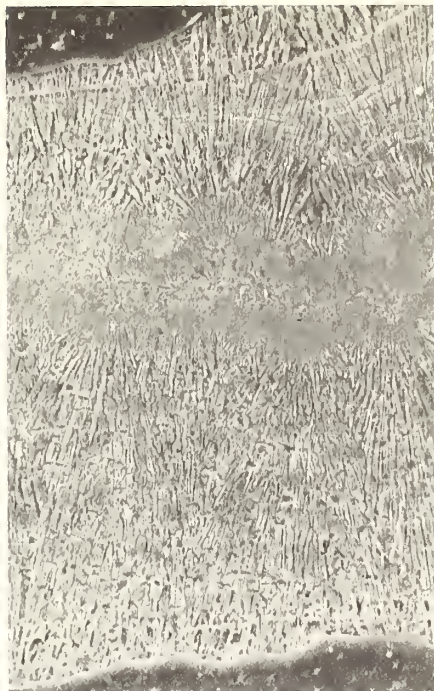
In transverse thin sections of septa in a branch corallite, it can likewise be noted that the 'dark line' is not uniformly developed as an axial plane that is apparent in all septa (Pl. 4, fig. 1), as commonly the trabecular centres are only weakly developed. However, when the trace of a septal axis is followed back into the theca, well-defined and well-rounded trabecular centres can be seen clearly developed, but of extremely small diameter (Pl. 4, fig. 2). This is the position of maximal septal growth, where septa are exsert, and additionally, in this position the cross-section is perpendicular

EXPLANATION OF PLATE 3

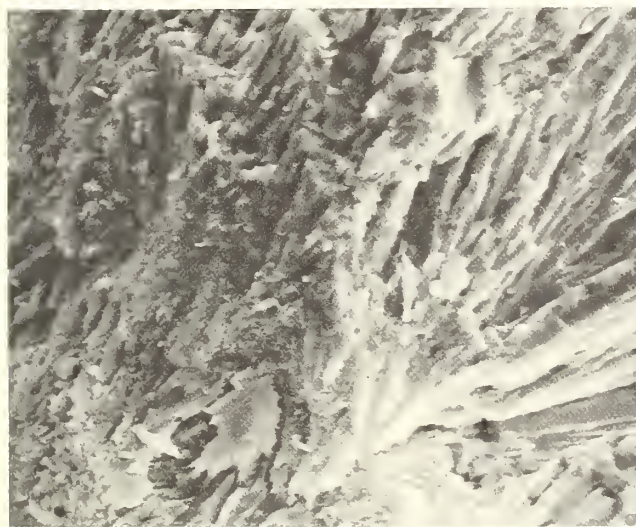
Figs. 1-5. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, view of broken section through lateral portion of septum with interfering clusters of crystallites growing toward smooth septal flanks, $\times 200$. 2, enlarged view of one crystallite fan, with what are apparently small crystals at apex and larger crystals further up from apex, $\times 1000$. 3, small sub-rounded crystallites at apex of cluster, $\times 10\ 000$. 4, transverse section of septum with extremely fine crystallites forming centres of trabeculae and rather compact interfering crystal clusters forming the septal flanks, $\times 400$. 5, enlargement of the upper-left portion of fig. 4 illustrating growth lines, interference of cluster systems, and very finely crystalline nature of the trabecular centres, $\times 1000$.



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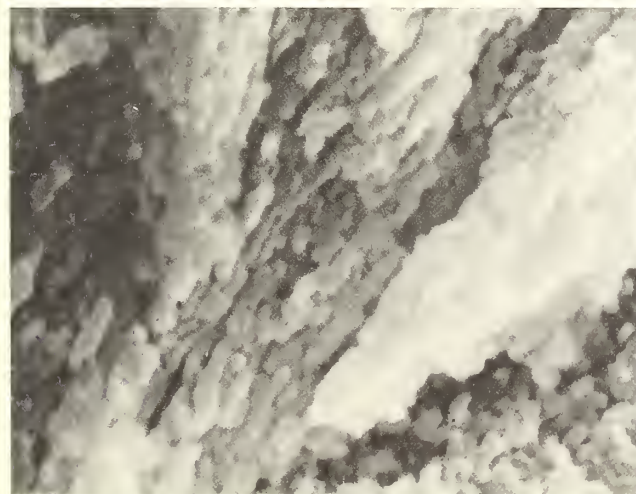
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to the trace of the trabecular axes. Orientation is thus playing an important role in allowing visual definition of the septal trabeculae.

Transverse thin sections in the stock of a budded corallite show that at first glance (Pl. 1, fig. 6; Pl. 4, fig. 3) it is difficult to distinguish septa from infilled interseptal spaces. The central portions of the corallite, where stereome is abundant, show crystallites filling the interseptal areas that are the same size and have the same orientation as those in the lateral part of the septum (Pl. 4, figs. 4, 5). They most simply represent continued crystallite growth into the interseptal spaces until all available space is occupied.

Longitudinal sections of the septa of *Desmophyllum* differ somewhat depending on whether the section passes close to the axial zone of the septum or the septal flank. In the latter case, the view is virtually indistinguishable from longitudinal sections through the theca.

The simplest geometrical arrangement of the very small diameter trabeculae (or trabecula-like bundles) is seen in longitudinal sections which pass close to but not directly along the axial zone of the septum. A section here (Pl. 5, fig. 1) shows several rows of trabeculae diverging from the general axial zone (right side), with small diameter trabeculae seen almost in longitudinal section here to the left of the laterally directed rows of trabeculae. Those trabeculae seen in longitudinal section are regarded as showing the main growth direction of the septa and forming the 'dark line', seen in photomicrographs (Pl. 5, fig. 2). The trabeculae seen in longitudinal section gradually bend or branch so that some crystallites grow perpendicular to the septal flank and form stereome indistinguishable from that infilling interseptal spaces and forming theca (Pl. 5, fig. 4). Where micrographs include a portion of the septal flank material, the 'dark line' of fine trabeculae is interrupted by the presence of larger, parallel crystallites with growth lines within them (Pl. 5, fig. 3). In these sections, it should be noted that there is only an important and easily visible growth line between trabeculae and septal stereome. This is as noted previously in transverse sections (Pl. 4, figs. 4, 5). This is also shown (Pl. 5, figs. 1 and 4; Pl. 6, fig. 3) where trabeculae are seen grading into bundles of larger crystallites which in turn grade into stereome with ill-defined trabecular centres.

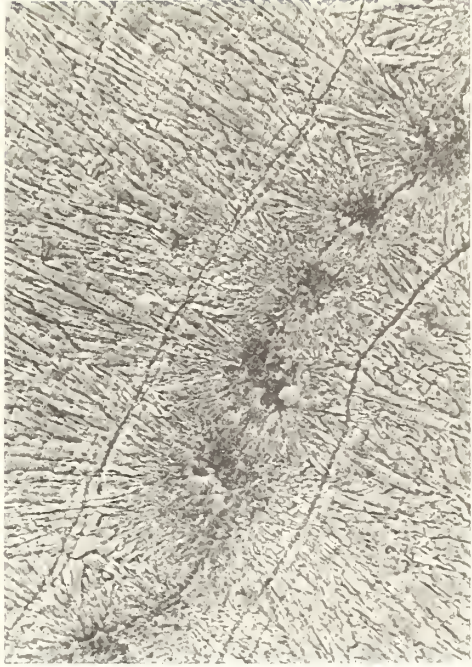
In longitudinal sections paralleling and closely approximating the path of the axial plane of the septum, much more divergence of rows of trabeculae is seen. As was noted previously, in broken sections regular rows of trabeculae diverge from

EXPLANATION OF PLATE 4

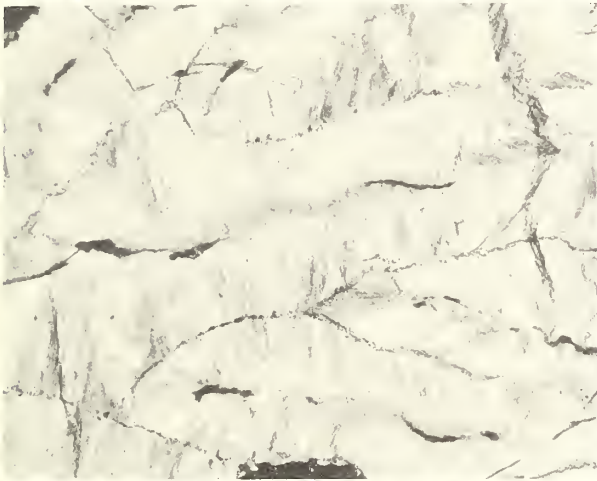
Figs. 1-5. Photomicrographs (1, 3) and scanning electron micrographs (2, 4, 5) of *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, photomicrograph of septa and theca in immature portion of corallite with central dark line in septa and also with dark line of divergence outlining centre of early septotheca, crossed nicols, $\times 63$. 2, transverse section within theca showing clear development of septal trabeculae, $\times 1000$. 3, transverse thin section of stock of budded corallite showing complete filling by crystallite growth, with interseptal spaces difficult to differentiate from septa, crossed nicols, $\times 63$. 4, overview of septum in transverse section with continued crystal growth over prominent growth line into interseptal space, $\times 500$. 5, enlarged portion of fig. 4 showing that crystal orientation and position does not change from septum (on right) into lumen. Margin of septum is marked by prominent growth line, $\times 2000$.



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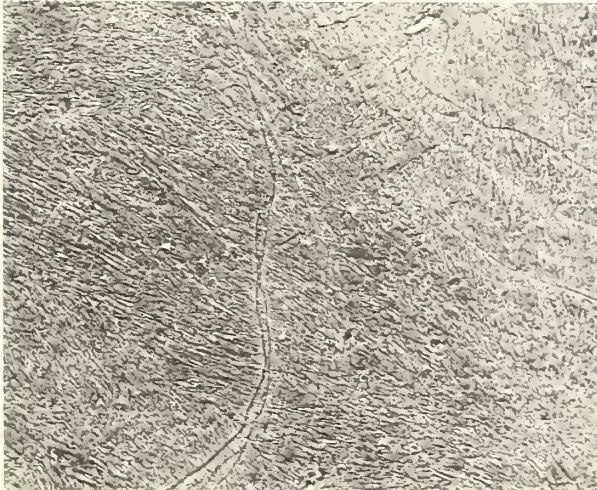
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the axial zone and bend outward toward the septal flank. These lateral outgrowths are in the form of diverging clusters and interfere with each other within the same generation, as well as with other rows of clusters (commonly overgrown).

Two types of growth lines are seen, one a line occurring on individual crystallites (Pl. 8, fig. 1), in which etching exaggerates a crystal discontinuity, and a second type formed by rows of diverging trabeculae. This bending of trabeculae out of the axial plane of the septum produces striking and informative polished and etched sections.

Growth parallel to the axial zone, with large crystallites, is common (Pl. 6, fig. 2) with growth punctuated by easily identifiable growth lines. At the top of this sequence can be seen a breaking down of large crystallites into smaller branching crystallites. This row of branching crystallites is then followed by one or more rows of trabeculae which diverge at a high angle from the axial plane forming a striking visual discontinuity with pre-existing crystal clusters (Pl. 6, figs. 2-4). This may well be the type of discordance where the row of tufted crystallites is seen overgrown by the overlying trabeculae (Pl. 6, fig. 4) or there can be a bending of the row of tufted crystallites to form trabeculae (Pl. 7, fig. 1). The discordant arrangement is commoner in our material with layers of trabeculae and overgrown crystallites (Pl. 6, fig. 4). Crystal sizes generally present at the corners of junctions of trabeculae are generally slightly larger than usual, perhaps an indication of additional space for growth. In this figure, the approach towards stereome at the left of the micrograph is shown by the presence of larger crystal sizes at the side of the micrograph.

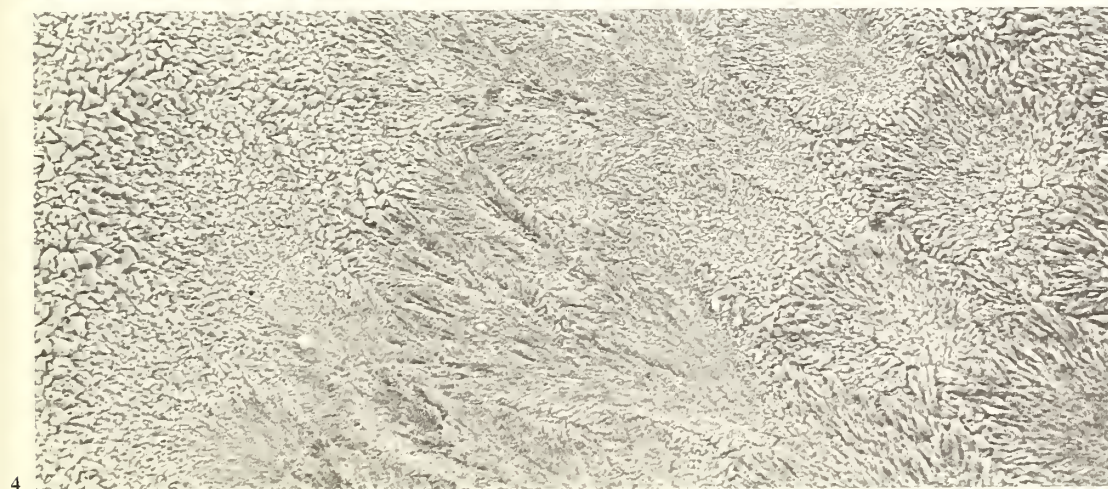
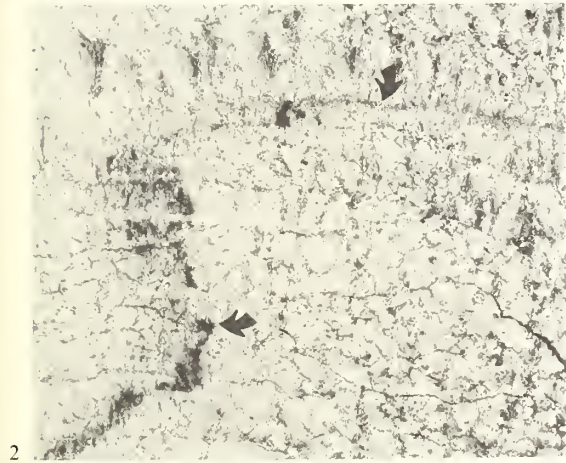
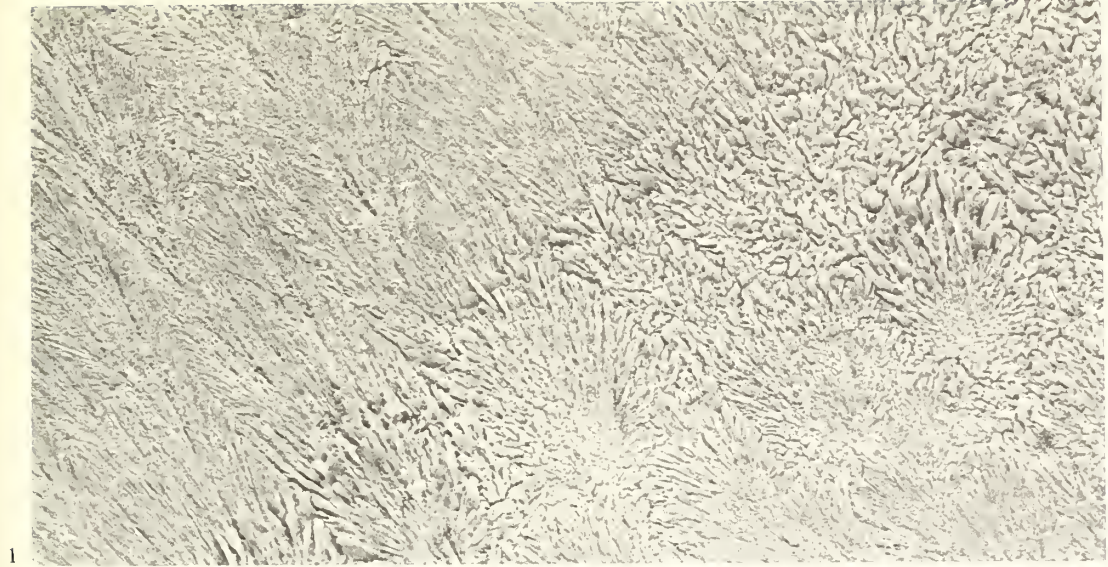
In the inner septal stereome of the flank, there is a rapid increase in the diffuseness of the trabecular centres as distance from the axial plane increases (Pl. 7, figs. 2, 3).

Stereome, thecal. One of the striking characteristics noted in the subfamily Desmophyllinae (especially in *Desmophyllum* and *Lophelia*) is the presence of a wall and septa thickened by deposition of stereome (secondary biogenic aragonite). This section deals with the thick outer wall, characterized by dense stereome.

In thin sections of young individuals, it can be seen (Pl. 1, fig. 5; Pl. 4, fig. 1) that a dark line surrounds the calice and is apparently identical to and in places contiguous with the dark line of septa. The dark line in the theca results from the intersection of the plane of the thin section with a cylindrical zone of divergence of growing crystallites. This line, referred to here as the calicinal dark line, may be analogous to the septal 'dark line' (or axial zone), but it is apparently not trabecular in nature.

EXPLANATION OF PLATE 5

Figs. 1-4. Photomicrograph (2) and scanning electron micrographs (1, 3, 4), *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, longitudinal section close to axial plane of septum with individual trabeculae easily distinguishable where they diverge from the axial plane (at right) and more difficult to isolate where they more closely parallel the septal plane, $\times 1000$. 2, somewhat oblique longitudinal thin section illustrating somewhat smeared out central dark line (arrow), crossed nicols, $\times 63$. 3, longitudinal section showing coarser crystallites developed parallel to, but away from axial plane where plane is wrinkled (thus more distant at this position), $\times 1000$. 4, longitudinal section showing trabeculae paralleling axial plane at right centre and gradually bending out to form stereome (at left) without trabecular centres, $\times 1000$.



It can be seen that where septa and theca intersect (Pl. 4, fig. 2) septal trabeculae are readily distinguished from the 'dark line' in the theca resulting from divergence of crystallites.

Photomicrographs (Pl. 1, fig. 5; Pl. 4, fig. 1) show a definite discontinuity exterior to the calicinal dark ring. This discontinuity is apparently the result of contrast between inner, more ordered, dense aragonite crystallite clusters, and an outer, less orderly secondary biogenic stereome added to the maturing corallite. As can be seen in photomicrographs (Pl. 1, fig. 5), the outer wall is totally composed of semi-continuous crystallite clusters with axes of calcification perpendicular to the surface of the theca and divergence of crystallites from the axes. These differ from septal trabeculae mainly in their lack of discrete centres of finer crystallites. The stereome is composed of crystal clusters growing in subparallel arrangement, as in septal thickening (Pl. 7, fig. 3) and it is only in the interior portions of the wall that axes of divergence are clearly noted (Pl. 7, fig. 4) and a short distance from the axial plane one is hard put to identify such organization in tangential section.

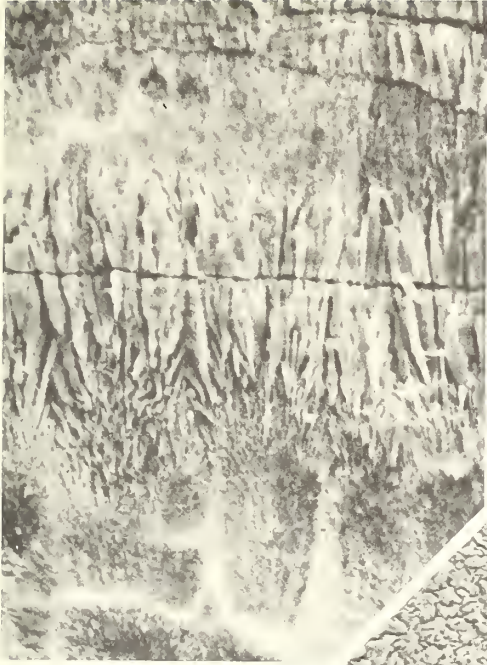
The outer surface of the wall of *Desmophyllum* is granulated but with a smooth microarchitecture (Pl. 7, fig. 5) and normally no individual crystallite ends can be seen even at magnifications of several thousand times natural size. However, in the area between the septal ridges at the top of corallites, crystallite growth edges are readily apparent (Pl. 8, figs. 1, 2). This area is occupied by the edge zone of the coral (according to Squires 1959, p. 19), and is obviously where continuing calcification and thickening of theca is occurring.

Stereome, calicinal filling. Our specimens of *Desmophyllum* are characterized at least partially by infilling of interseptal spaces, presenting the aspect of having the entire lumen filled with stereome in earlier stages (Pl. 1, fig. 6; Pl. 4, fig. 3). It may be that this characteristic is a basal support method at times alternative to development of tabular dissepiments such as seen occasionally in adult *Desmophyllum* and as described previously in *Lophelia* (Sorauf 1970, p. 11). Such complete infilling is also seen in the solitary genera *Flabellum*, *Caryophyllia*, *Balanophyllia*, and *Thecosamnia* (Sorauf and Podoff, in press).

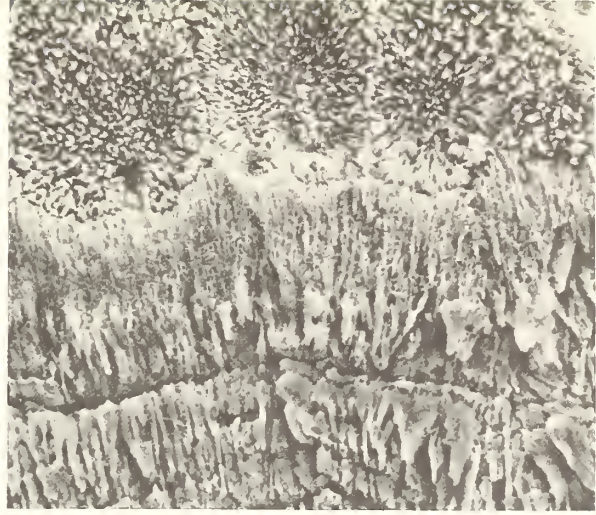
Septal thickening is due to continued growth of aragonite crystallites which lose their well-defined centres of calcification as distance from the axial zone increases (Pl. 7, figs. 2, 3). In a polished and etched section of a stereome-filled corallite (Pl. 4,

EXPLANATION OF PLATE 6

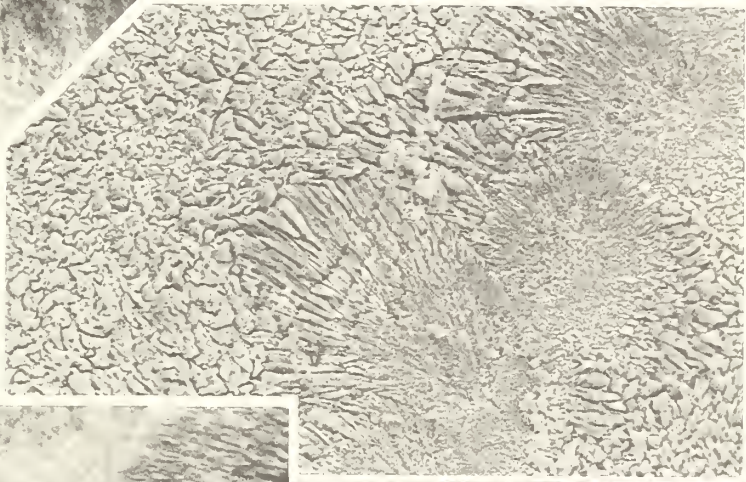
Figs. 1-4. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, longitudinal micrograph with marked growth lines (exaggerated by etching) cutting straight across crystal growth direction, $\times 1000$. 2, longitudinal section showing growth lines as in fig. 1, but also illustrating growth discontinuity by overgrowth of trabeculae at top that have diverged greatly from the axial plane and the apparent increased number of smaller crystals at the top of the growth cycle below the discontinuity, $\times 1000$. 3, longitudinal section parallel to but at a distance from the axial zone of the septum, with trabecular centres not distinguishable within septal stereome at left, $\times 1000$. 4, longitudinal section showing trabeculae, changing orientation angles, and rather sharp discontinuity with overlying crystal clusters, $\times 2000$.



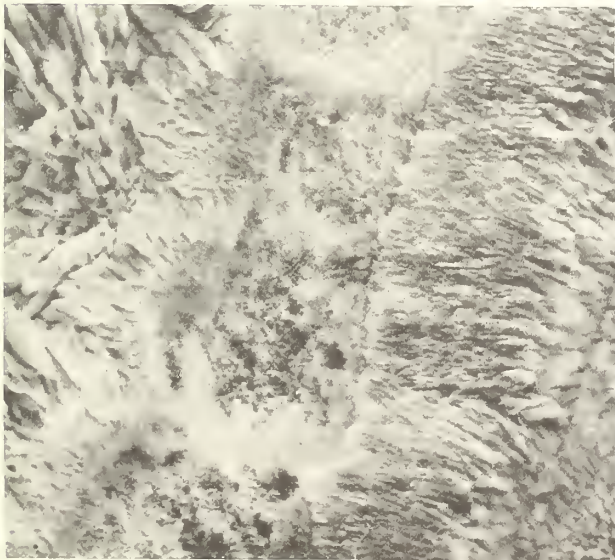
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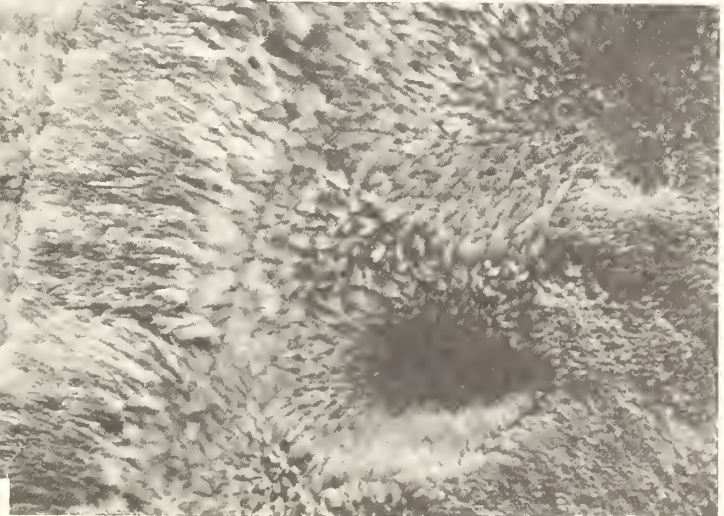
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figs. 4, 5) the interseptal stereome is seen formed by continued epitaxial crystal growth out from septal flanks. Growing crystallites join at a midline with those growing out from a neighbouring septum. Thus, the mass of infilling crystals is distinguished in crystallite size and habit from those in septal flanks only by the presence of more prominent growth lines in the latter. There is apparently a halt in crystal growth when the septum is completed, with later overgrowth occurring with the same size, shape, crystallographic orientation, and position as those crystals forming the septal flanks.

This form of crystal growth and the characteristic of forming a continuous floor to the calice is shared with *Lophelia* and other members of the family group that are characterized by tabular dissepiments. As previously noted (Sorauf 1970), the dissepiments in *Lophelia* are formed of a sheet of crystallites that are continuous with those sheets that thicken septa. In *Desmophyllum* dissepiments with a continuous blanket of crystallites occur occasionally, as well as the complete infilling by stereome in early stages.

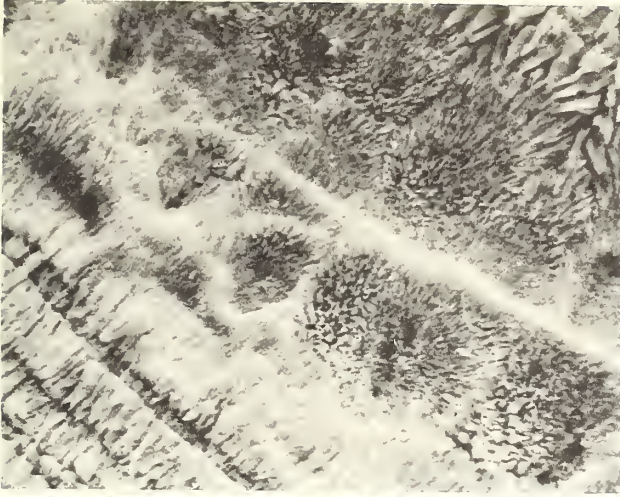
Dissepiments. Dissepiments are sparse but present in each of the large corallites in our sample. The dissepiments are very similar to those of the *L. prolifera* described by Sorauf (1970, p. 11). As seen in scanning micrographs, the dissepiments completely fill the interseptal spaces (Pl. 8, fig. 3), thus are referred to as tabular dissepiments. As seen from the upper or distal side, the surface is more or less featureless, and is composed of a carpet of small crystallites growing approximately perpendicular to this surface (Pl. 8, fig. 4). The septal thickening (stereome) on the flanks of the septa appears to be continuous with the upper layer of crystals on the dissepiments, just as in *L. prolifera*.

The under surface (proximal) is characterized by a prominent central junction groove, and weak growth lines (Pl. 8, fig. 5), and at higher magnifications, this under surface is seen to be formed by laterally growing, centrally directed, weakly bundled crystallites (Pl. 8, fig. 6).

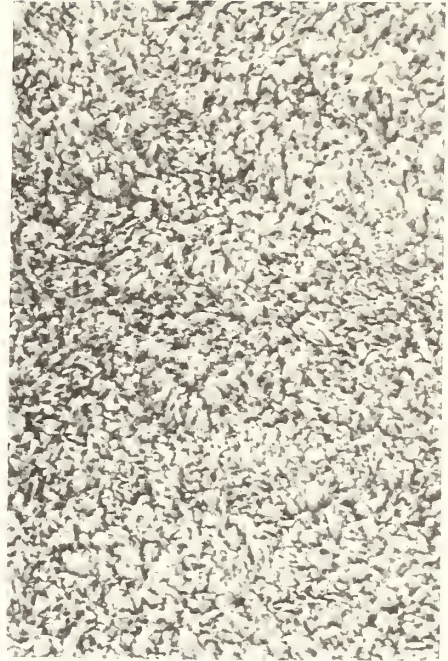
Thus, in all major aspects these dissepiments are similar to those of *Lophelia*, colonial ahermatype closely related to *Desmophyllum* and also found in deep waters of the Atlantic. The main variation between the two is the occurrence of stereome infilling the calices of small diameter, budded corallites in *Desmophyllum*; tabular dissepiments are more sparse in *Desmophyllum*, and apparently restricted to adult corallites.

EXPLANATION OF PLATE 7

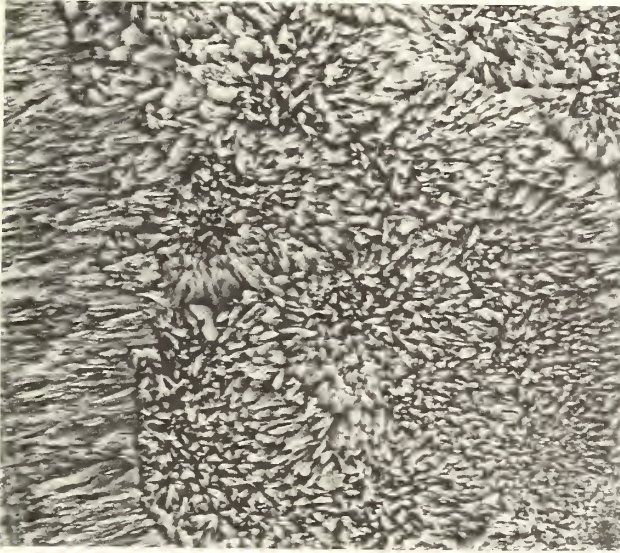
Figs. 1-5. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, somewhat oblique longitudinal section to illustrate appearance of trabeculae which are parallel to the axial plane at the lower left, but are above bent out at a considerable angle of deflection, $\times 1000$. 2, longitudinal section showing transition into septal stereome in which trabecular centres are still discernible, $\times 500$. 3, longitudinal section of crystallites in septum growing in subparallel fashion perpendicular to plane of etched section, $\times 500$. 4, transverse view of early part of theca to illustrate one single row of crystal clusters growing towards former margin, here with manganese (?) crust not etched by EDTA, $\times 300$. 5, individual granulation on outer flank of theca, $\times 2000$.



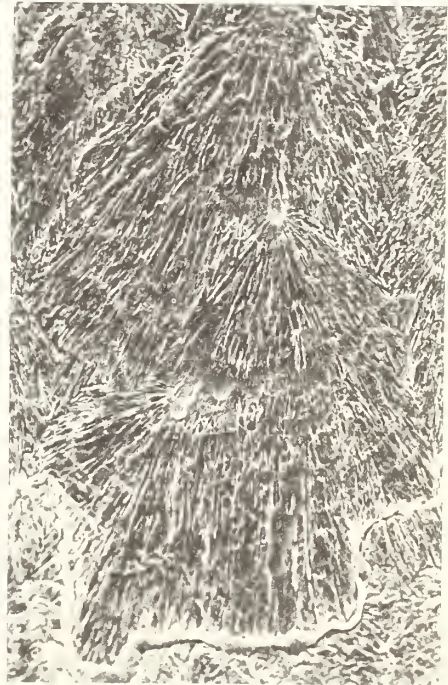
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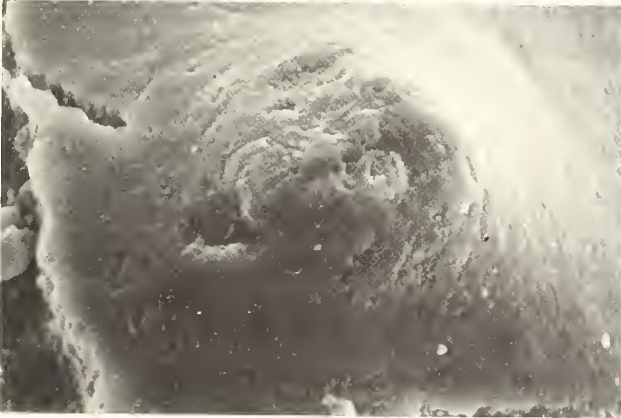
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INCREMENTAL GROWTH

Apparent wrinkling in the axial zone of septa has been shown to be an artifact of breaking rows of rapidly expanding (laterally diverging) crystallite clusters. It seems apparent that the coral exoskeleton is being formed at varying rates, and that an increase in crystallization rate causes a lateral expansion of a crystallite cluster system, with very fine trabeculae formed. These most commonly overgrow pre-existing trabecular groups with an apparent discontinuity (Pl. 2, figs. 2, 3; Pl. 6, figs. 1, 2, 4). This lateral growth then reflects times of more rapid calcification, alternating with times of slower accretion represented by lesser developed clusters.

Such incremental growth is also noted in trabeculae, dissepiments, and stereome. Growth lines (as opposed to the septal wrinkling) are also noted within the crystals forming flanks of septa (Pl. 3, figs. 4, 5) and growth 'rings' are seen in the thecal stereome (Pl. 1, figs. 5, 6). These growth increments are at the least episodic and apparently periodic, since the size of increments is rather uniform for any single skeletal element.

Periodic incremental growth in hermatypic, shallow-water corals is strongly influenced by the presence of symbiotic zooxanthellae (Goreau 1959). However, Goreau also found that calcification in hermatypic corals did continue during periods of darkness, although at a lesser rate apparently connected to inactivity of the zooxanthellae, and was able to conclude that the secretion of the enzyme carbonic anhydrase is important in the calcification of the hermatypic skeleton. It should perhaps also be supposed that deep-water-dwelling ahermatypic corals, forming skeleton under adverse conditions of low carbonate concentrations, low temperatures, and high water pressures without the aid of algal symbionts, must have a remarkable ability for enzyme production to aid in the calcification process.

Wells (1970, p. 7) has discussed the growth periodicity in ahermatypic corals as well as in hermatypic forms. He has assumed that periodic growth in both groups has the same underlying control or set of controls. Possible causes were listed as follows: 1, daily fluctuations in nutrient supply; 2, daily tidal flux; 3, daily temperature variations; 4, diurnal variations in terrestrial magnetism; and 5, biological clock control.

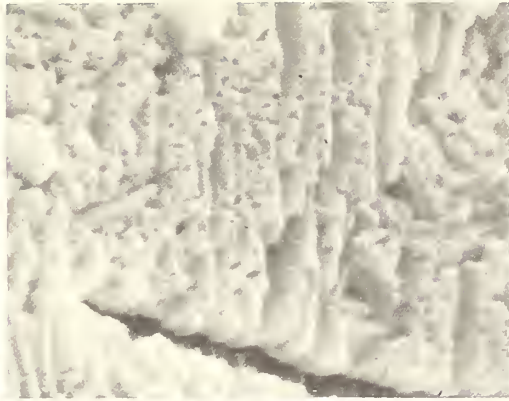
Of these, only the latter two are considered as potential controls in the case of the *Desmophyllum* specimens discussed here. The effect of variations in terrestrial

EXPLANATION OF PLATE 8

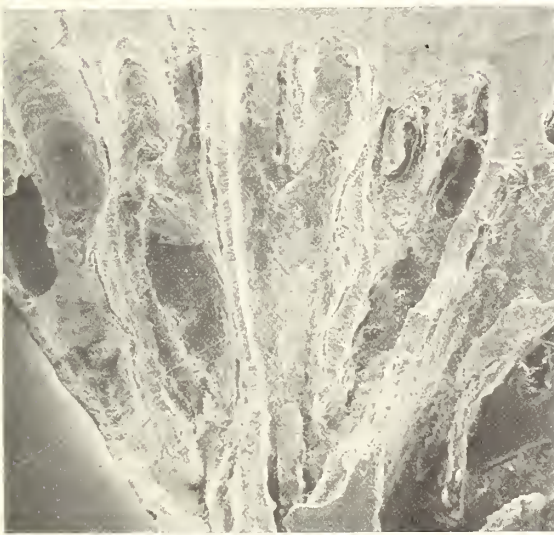
Figs. 1-6. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, exterior of theca near calicinal termination illustrating septal costa and interseptal area with crystal faces developed. Note also boring in this portion of specimen, $\times 1000$. 2, enlargement of crystal faces in interseptal area, $\times 5000$. 3, overview of upper (or distal) side of dissepiments which completely fill area between septa, here broken away to expose featureless upper surface of dissepiment, $\times 22$. 4, enlarged view of crystal carpet forming upper surface of dissepiment, $\times 2200$. 5, overview of underside (proximal side) of dissepiment illustrating the central junction groove and weak growth lines on this surface, $\times 50$. 6, enlargement of undersurface illustrated in fig. 5, showing weakly bundled nature of crystallites growing from septum in lower-right corner of micrograph to junction groove at top left of micrograph. Note too the weak development of growth ridges, $\times 240$.



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magnetism cannot at present be evaluated. The last, a biological clock control, seems possible, and may be connected with enzyme production tied to a feeding cycle based on energy requirements of the coral polyps. These requirements would by necessity be inherited, thus the feeding cycle would also be inherited in a sense, although perhaps with considerable modification. The growth increments noted here within *Desmophyllum* are in the proper size range to be diurnal, but as yet there is no real proof that they are in fact diurnal, whether in the sense of a 24-hour day or in the sense of an 'inherited' day of other than 24 hours.

CONCLUSIONS

D. cristagalli as represented by the material available to us has a certain number of skeletal characteristics which may prove helpful both in recognizing allied genera in the fossil state, and also in interpreting structures seen in other groups of fossil corals. Eventually it is hoped that knowledge of structure may help define extinct groups of ahermatypic corals and aid in the environmental interpretations of coral-bearing strata.

D. cristagalli has the following:

1. Septal structure which is similar to that recognized as fibro-normal in fossil corals. It is supposed that the very fine septal trabeculae in genera such as *Desmophyllum* would be easily obliterated during diagenesis, resulting in a truly fibro-normal structure.
2. Wrinkling along the septal axial planes caused by the divergence of rows of fine trabeculae out of the axial orientation and into an orientation normal to the axial plane. Such extreme bending of trabeculae is abnormal for corals with trabeculate septa. This wrinkling is apparently periodic and a reflection of incremental growth.
3. Development of a covering of stereome thickening both the theca and the septa, commonly resulting in the complete infilling of the basal portion of the corallite. The formation of this secondary biogenic blanketing of all skeletal features creates a definite unity of skeletal structure, more than typical for scleractinian corals. This unity is also noted in some other ahermatypic corals.

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THE LAMINAE AND CUTICULAR ORGANIZATION OF THE TRILOBITE *ASAPHUS RANICEPS*

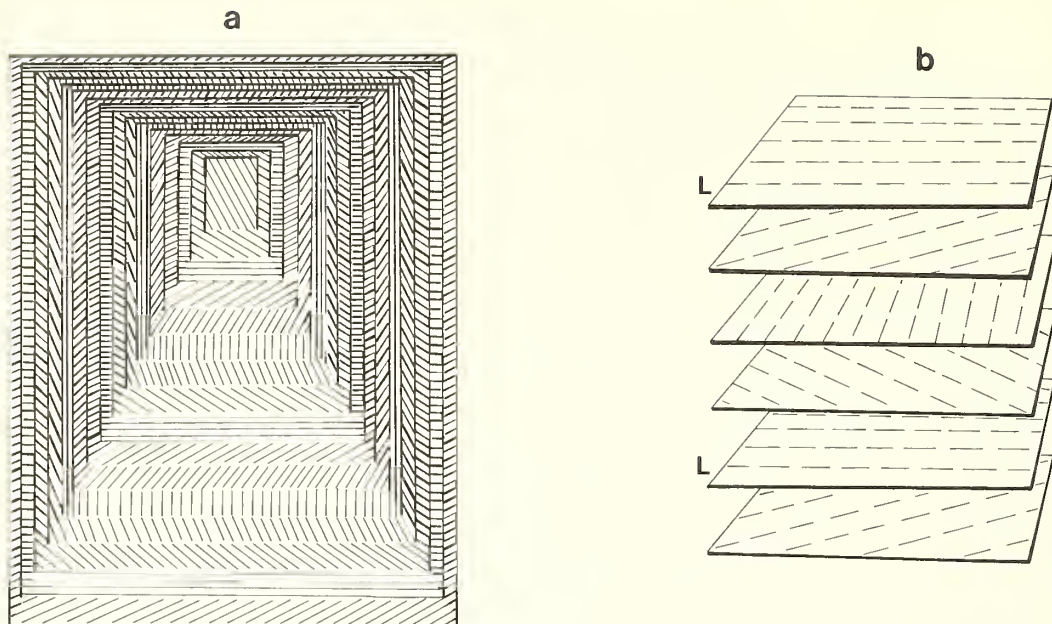
by J. E. DALINGWATER and J. MILLER

ABSTRACT. The cuticle of *Asaphus raniceps* Dalman has been examined with the scanning electron microscope after preparation by breaking and etching. Three main zones are defined on differences in appearance and dimensions of laminar units. Some details of the fine structure of laminar units are described. The presence of an organic framework within the cuticle is confirmed. The laminae and organization of the cuticle of this species are considered comparable to those of many extant arthropod cuticles.

RECENT work has presented a general picture of the microstructure and composition of the trilobite cuticle (Dalingwater 1973; Teigler and Towe 1975), as well as a consideration of the possible functions of cuticular organs (Miller 1975, 1976). Much of this work was based on optical examination of thin sections; Teigler and Towe (1975) also studied some aspects of the cuticle with the transmission electron microscope (TEM). Recently, we have prepared trilobite cuticles for study with the scanning electron microscope (SEM) by cutting and etching or by fracturing; fracturing followed by etching proved to be a most effective technique.

Laminae are a particularly prominent feature of some well-preserved trilobite cuticles prepared by this method. Most extant arthropod cuticles when viewed in cross-section show a laminar structure, usually visible as sets of alternating dark and light bands (Richards 1951). Whilst laminar units have been recognized in optical microscope preparations of trilobite cuticles by many previous workers (see Rolfe 1962; Dalingwater 1973) generally they are not very clearly visible. They have often been described as narrow bands although occasionally wider laminar units have been recognized, for example by Størmer (1930). Teigler and Towe (1975) recognized a crudely layered aspect to the crystals making up the cuticles of some of the trilobite species which they studied but did not consider it to be true lamination. For this reason, and others discussed below, they concluded that the trilobite cuticle did not have a laminate aspect comparable with that of the majority of extant arthropod cuticles but more strongly resembled the architecture of the calcified ostracod cuticles described by Bate and East (1972).

There has been much recent controversy as to the reality of laminae in extant arthropod cuticles. The view of Bouligand (1965, 1972) and of Neville and his co-workers (1969) that the laminate appearance of cuticles is an artefact resulting from sectioning helicoidally arranged flat sheets of fibres (text-fig. 1) had, until recently, been supremely ascendant over the traditional view of laminae as real structures. Recent papers, notably those of Dennell (1973, 1974) and Mutvei (1974), have re-emphasized the reality of laminae and thereby revived the controversy. Nevertheless, all these authors agree that laminae, real or artefact, at least reflect



TEXT-FIG. 1. Bouligand helicoidal model (re-drawn, after Bouligand 1965, 1972). *a*, truncated pyramid of cuticle viewed from above. Flat sheets of fibres are arranged in stacks and the fibre orientation changes from one sheet to the next in an anti-clockwise direction. *b*, simplified 'exploded' view of the system. Apparent laminae (L) result when sheets of fibres are sectioned parallel to fibre orientation, i.e. in the plane of the page.

a repetitive layered organization which is a fundamental feature of nearly all arthropod cuticles. Furthermore, important subdivisions of cuticles are often reflected by differences in laminar aspect, for example in the dimensions of laminar units.

In this paper:

We indicate that laminae and canals in some well-preserved trilobite cuticles can be demonstrated particularly well by the technique described.

We define three zones in a trilobite cuticle distinguished by differences in laminar disposition, correlate these with the subdivisions of the cuticle established by Dalingwater (1973) and Teigler and Towe (1975), and compare the subdivisions of the trilobite cuticle with those of extant crustaceans.

We present a case for considering the laminae of the species studied, and by implication those of some other previously described trilobite species, as similar to those of many extant arthropods. Particularly in this respect, we question Teigler and Towe's (1975) interpretation of the trilobite cuticle as more similar to that of some calcified ostracods than to that of the typical arthropod.

We advise caution in adopting Teigler and Towe's (1975) use of the term *pore canal* for all categories of primary ducts through the trilobite cuticle.

MATERIALS AND METHODS

We have examined the cuticles of a variety of trilobite species after preparation by the method described below, including those of:

Iliaenus aduncus, lower Ordovician, Öland.

Iliaenus sarsi, lower Ordovician, Oslofjord.

Omia sp., upper Ordovician, Onny River, Salop.

Tretaspis spp., upper Ordovician, Oslo.

Calymene blumenbachii, middle Silurian, Dudley, West Midlands.

Phacops rana subsp., middle Devonian, Ohio.

P. rana africanus, middle Devonian, Rio de Oro, Tifariti.

Harpes macrocephalus, middle Devonian, Gerolstein.

Although laminae and other microstructural features were seen in all the cuticles examined, the most immediately striking results were obtained from the cuticle of *Asaphus raniceps* Dalman *sensu* Angelin (1854) from the lower 'Raniceps' Limestone, Haget, Öland, Sweden (lower Llanvirn—*bifidus* Zone), particularly from specimens with dark chocolate brown exoskeletons collected from bed 'e' of Bohlin (1949). We therefore concentrated our attention on this material.

Fragments of cuticle were removed from various regions of the exoskeleton, rebroken to produce as clean a fracture surface as possible, and then etched for about one hour in a saturated aqueous solution of E.D.T.A. (disodium salt). After rinsing with distilled water, they were then washed in absolute alcohol several times and mounted on stubs. Preparations were gold or gold/palladium coated before examination with the SEM. Fragments of cuticle from a thoracic limb podite of the fossil decapod crustacean *Hoploparia longimana* (Sowerby) from the Cambridge Greensand, figured and discussed below, were prepared in a similar manner to the trilobite material, but etched for about three hours in E.D.T.A. Cuticle from the great chela of the extant decapod crustacean *Austropotamobius pallipes* (Lereboullet) was prepared as described in Dalingwater (1975). All figured preparations are stored in the Department of Zoology, University of Manchester.

TERMINOLOGY

The major textural subdivisions of the trilobite cuticle previously recognized were an outer layer often prismatic, and an inner or principal layer (Dalingwater 1973; Teigler and Towe 1975). Subdivisions of the cuticle described herein, based on differences in appearance and dimensions of laminar units, are termed zones. Correlation between the layers and zones is discussed later.

Following Dennell (1973), we refer to the narrow part of each laminar unit as a lamina and the wider part as an inter-lamina. In some crustacean cuticles laminae appear to consist of sheets of horizontal fibres, and inter-laminae of sheets of fibres which arc between successive laminae (Dalingwater 1975). Dennell (1976) has demonstrated the presence of a lamina membrane in the cuticles of a variety of arthropods, and suggests that it might provide a template for laying down the cuticular fibres.

OBSERVATIONS

Cuticle zonation. The appearance of etched fracture surfaces of *Asaphus raniceps* cuticle varies somewhat in different preparations possibly due to slight differences in the method of preparation (including angle of break) and/or in preservation. There are also slight but consistent differences in the cuticle from different parts of the exoskeleton. Nevertheless, a general outline of the appearance of the cuticle when examined with the SEM can be given. The outermost part of the cuticle is etched back very rapidly and was therefore not often visible in our preparations. Below this, various zones can be defined based on differences in appearance and dimensions of the laminar units:

An outer zone of narrow laminar units (around 5μ thick) comprising up to one-fifth of the total thickness of the cuticle.

A central zone of four or five very prominent wide laminar units ($50\text{--}70\mu$) grading inwards through a zone of less prominent wide laminar units into;

a narrow innermost zone of fine laminar units of similar dimensions to those in the outer zone.

The outer finely laminated zone tends to be most readily seen, and is possibly best developed, in preparations of thoracic pleurae (Pl. 9, fig. 1). In contrast, it often seems narrower in preparations of cephalic cuticle (Pl. 10, fig. 1). In some preparations there is apparent discontinuity of laminar units between the dorsal part of the exoskeleton and the doublure (Pl. 10, fig. 1).

Individual calcite crystals are difficult to resolve, but roughly shaped perpendicular plates of calcite are prominent in the wider inter-laminae, in some cases pierced by canal-like elements about 1μ wide (Pl. 9, fig. 2). In angled breaks these plates of material stand out as pillars separated by a network of voids (Pl. 9, fig. 3).

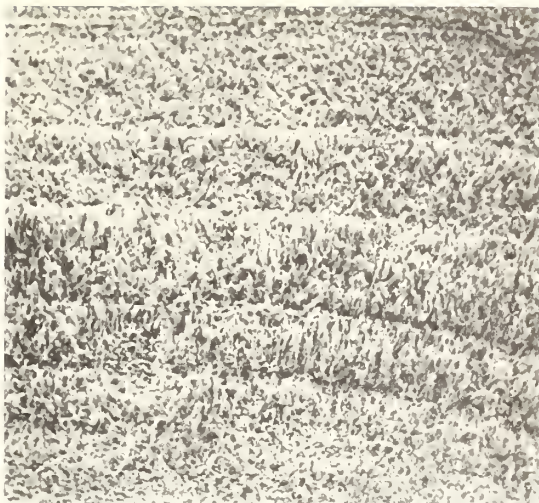
Structure of laminar units. In many preparations the laminae themselves appear as narrow co-planar bands which have been etched inwards more rapidly than the intervening material (Pl. 9, fig. 4). However, in some cases laminae are represented by wider bands of material, crossed by similar fine perpendicular canal-like structures to those in the inter-laminae (Pl. 9, fig. 5). Occasionally, traces of a rough chevron pattern can be perceived at the laminae (Pl. 9, fig. 6), and in one preparation faint

EXPLANATION OF PLATE 9

Figs. 1-6. *Asaphus raniceps* Dalman: scanning electron micrographs of etched fracture surfaces of the cuticle. 1, longitudinal perpendicular break across a thoracic pleura. Outer fine laminate zone clearly visible. Prep. 21375-3. $\times 170$. 2, detail of the central zone from the same preparation, showing perpendicular canal-like elements in the inter-laminae. $\times 210$. 3, tangential angled break across the edge of the cephalon. Central zone. Roughly shaped pillars of calcite stand out, separated by a network of voids. L—lamina. Prep. 11174-1. $\times 420$. 4, transverse perpendicular break of cephalic cuticle. Central zone. Laminae (L) have been etched inwards more rapidly than the intervening material. Prep. 21375-1. $\times 420$. 5, tangential perpendicular break of cephalic cuticle. Some central zone laminae are represented by wider bands of material. The narrow inner laminate zone can just be seen. Prep. 11174-2. $\times 140$. 6, tangential perpendicular break of cephalic cuticle. Faint horizontal fibres (arrowed) just visible below a lamina (L). Prep. 11174-2a. $\times 820$.



1



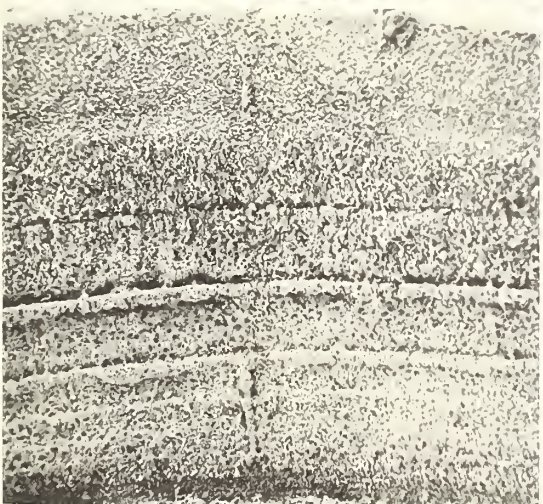
2



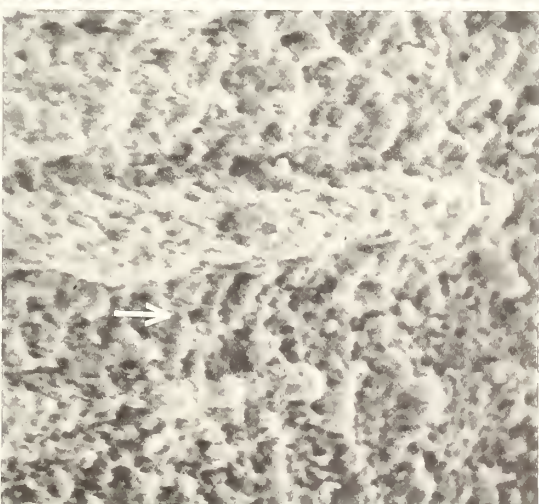
3



4



5



6

DALINGWATER and MILLER, trilobite cuticle

more or less horizontal fibres are visible in the plates of inter-lamina material just below a lamina (Pl. 9, fig. 6).

Decalcification of the cuticle. One exceptional preparation examined and photographed by reflected light microscopy (Pl. 10, fig. 2) deserves mention here. A thoracic pleura was removed from a large specimen of *A. raniceps* and a clean longitudinal perpendicular break achieved. Decalcification was allowed to proceed for five hours and the process observed at regular intervals. Laminae in the central zone of the cuticle were immediately apparent and some perpendicular ducts, about 5μ wide, could just be seen at this stage. After about five hours, much of the inorganic material of the cuticle had been dissolved inwards for some distance from the break surface leaving a layer of brown jelly-like material, with lighter-coloured material standing up through the gel at the laminae. The 5μ ducts could now be seen in depth piercing the brown jelly, their component material apparently unaffected by the E.D.T.A. Dissolution of inorganic material seemed greatest at the outer and inner zones of the cuticle, despite protection of the edges by adhering matrix.

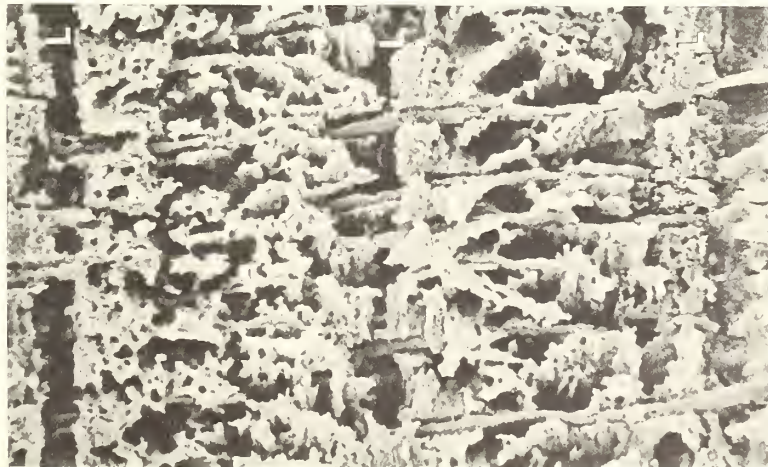
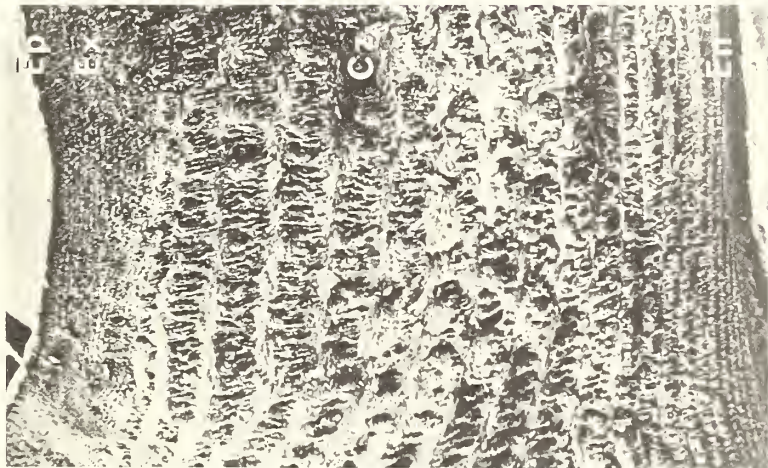
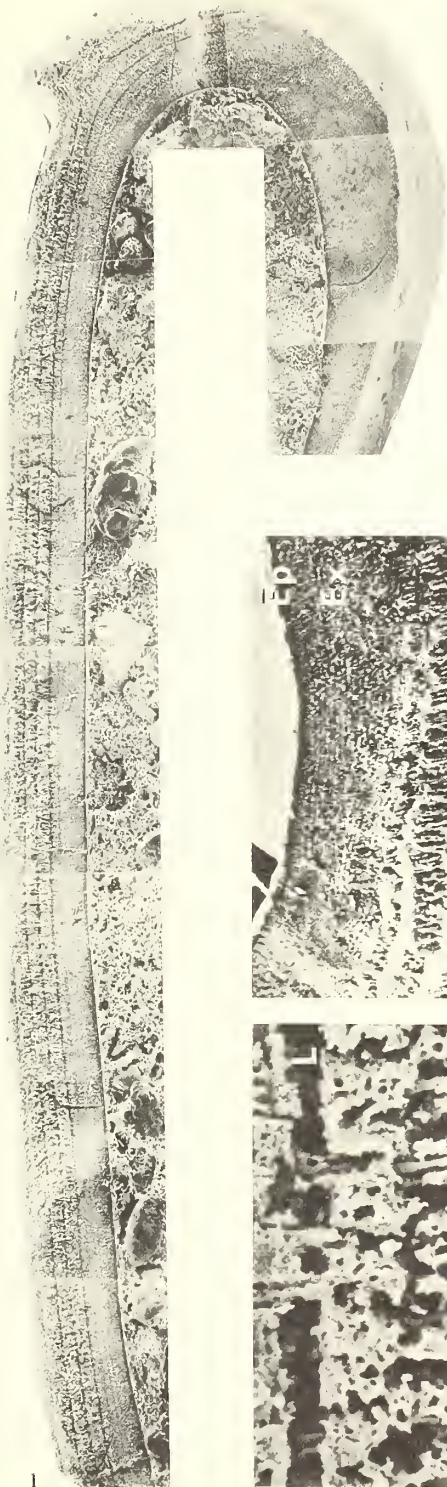
DISCUSSION

Laminae and pore canals. Teigler and Towe (1975) gave a number of reasons why the crudely laminate aspect of the calcite in some of the trilobite cuticles they examined should not be considered similar to the laminae in many extant arthropod cuticles:

1. Using the TEM they found no difference in the texture of the calcitic material at the laminae, only a slight furrowing, and decided that the laminae could have resulted from variation in the concentration of organic material within the cuticle rather than from some basic variation in the nature of the calcite crystals. However, laminae are essentially reflections of the organization of organic material within the cuticle; the essence of the lamina seems to be an organic lamina membrane (Dennell 1976). Miller's (1976) observation of flimsy organic membranes left representing the laminae while etching the cuticle of *Phacops rana*, as well as Teigler and Towe's comments on the distribution of organic material in the cuticles they studied, seem to indicate that in this context the laminae in trilobite cuticles can be seen to resemble those of many extant arthropods. The furrowing at the laminae in the cuticle of the fossil decapod crustacean studied (Pl. 10, fig. 3) strongly resembles

EXPLANATION OF PLATE 10

- Figs. 1, 2. *Asaphus raniceps* Dalman. 1, SEM photo-montage of a transverse perpendicular break of cephalic cuticle. The outer laminate zone can just be seen on the left. The wide laminar units of the central zone are prominent along the length of the preparation, except where the cuticle deflects to form the doublure. Prep. 21375-2. $\times 35$. 2, reflected light micrograph of a longitudinal perpendicular break across a thoracic pleura after about five hours decalcification. Prep. 191274-0. $\times 65$.
- Fig. 3. *Hoploparia longimana* (Sowerby). Transverse perpendicular break of the cuticle from a thoracic limb podite. Two laminar units in the calcified zone. L—lamina. Prep. H.s. 141175-1a. $\times 2100$.
- Fig. 4. *Austropotamobius pallipes* (Lereboullet). Transverse perpendicular break of the complete thickness of the cuticle from a great chela dactylopodite. Ep—epicuticle; Ex—exocuticle; Cz—calcified zone; En—endocuticle. Prep. A.p. 3376-2a. $\times 280$.



that seen in the trilobite cuticle. In both cases the absolute alcohol preparative treatment would remove any concentration of organic material from these furrows, for we have found that the organic residues left after complete decalcification of both trilobite and fossil decapod crustacean cuticles are completely dispersed by absolute alcohol. Incidentally, this might explain why well-preserved brown-coloured trilobite exoskeletons are 'whitened' by alcohol treatment.

2. They decided that the absence of helical pore canals and parabolic patterns also rendered difficult direct comparison with the usual extant arthropod cuticular laminae. However, pore canals are not necessarily helical (Travis 1970; Mutvei 1974), nor need their pattern be related to helicoidal architecture (Kennaugh 1965; Travis 1970; Dalingwater 1975). Even if the pore canals of trilobites were originally helical then this could have been altered in the process of fossilization (see discussion in Osmólska 1975). For example, only a straight contained filament or a straight lining might be preserved, with the canal itself (the lumen) infilled in the latter case. Parabolic patterns are only observed in angled sections (classically 45° sections) of extant cuticles, and only in *some* angled sections according to Drach (1939) and Dennell (1974). Many of Teigler and Towe's figured sections are more or less perpendicular slices; one would not expect parabolic patterns in such sections. Again diagenesis might alter the material and make recognition of parabolae in angled sections difficult.

3. They noted that not all trilobite species, even those from the same locality, show laminae, and concluded that a 'genetic control' appears to be the major factor in their distribution. We suggest that the precise history of preservation (see Miller 1975), and possibly the stage in the moult cycle reached before death in the case of intaglios, may determine whether laminae are prominent or even visible in examples studied. Methods of preparation and examination are clearly important: Dalingwater (1973) made an extensive investigation of the cuticle of *A. raniceps* using specimens from the same locality and horizon as those described above; he included an SEM examination of break surfaces and etched ground slices, but did not observe the distinct laminae that we have demonstrated by the break+etch technique.

We suggest that the evidence favours comparability of the laminae of trilobite cuticles, especially those of *A. raniceps*, with those of the typical arthropod cuticle.

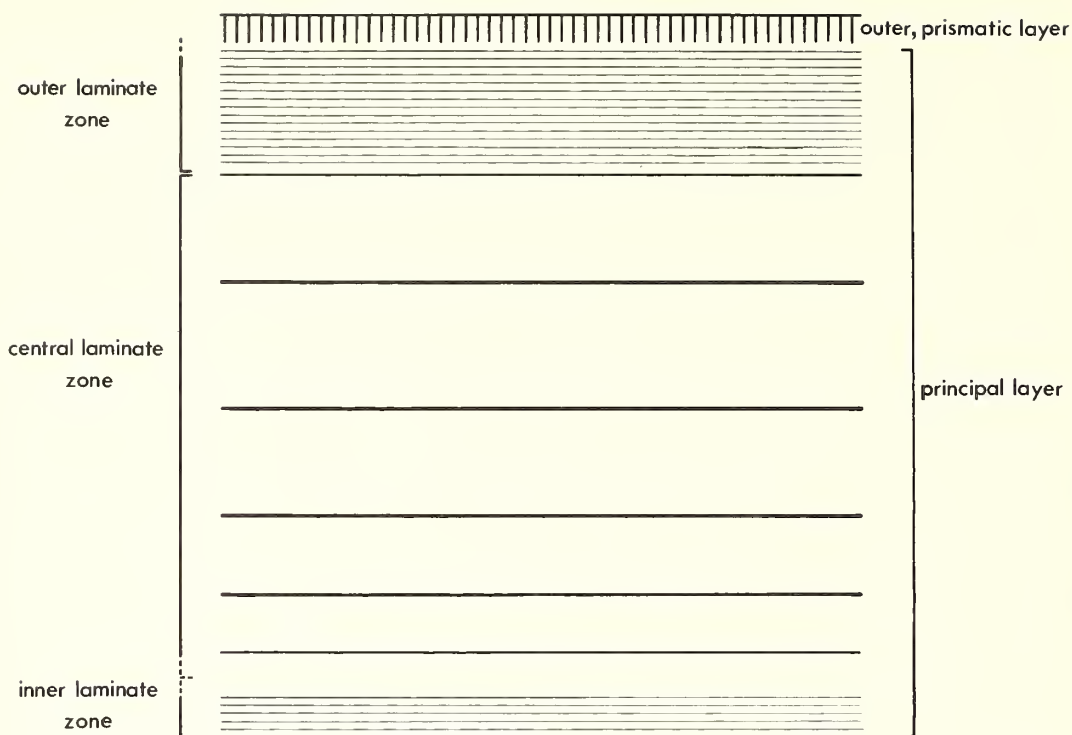
Some of the laminar units in *A. raniceps* cuticle are extremely wide (up to 70 μ) compared with those encountered in most extant cuticles, although in the crayfish *Austropotamobius pallipes*, laminar units about 20 μ wide are present in the calcified zone (Dalingwater 1975). However, the trilobite cuticle is usually relatively very thick for an arthropod often only a few centimetres long. These laminar units may represent material laid down rapidly after ecdysis (although it must be admitted that no evidence seems to have been presented correlating width of laminar unit with rate of cuticle formation). Finer co-planar structures within very wide laminar units have been reported from light microscope studies (e.g. Størmer 1930), and occasionally similar fine structures are encountered in SEM preparations. It is possible that these reflect the organization of inter-lamina material in low-angle arcs between laminae. The ultrastructural detail just recognizable in some preparations and described above tends to add strength to this view.

Perpendicular canals. Teigler and Towe (1975) termed all primary duct-like processes in trilobite cuticles *pore canals*. Whilst we recognize that it is difficult to decide whether canals of relatively narrow dimension (of the order of 1μ in diameter) are exactly equivalent to the pore canals of extant arthropod cuticles, or are merely unusually narrow tegumental or setal ducts, and that there is some imprecision in the definition of the pore canal even in extant cuticles, we are unhappy with Teigler and Towe's terminology. Canals 75μ and more wide are clearly not comparable with the pore canals of extant arthropod cuticles. Their proposal would place trilobite terminology in step with ostracod cuticle terminology, but out of step with that employed for all other arthropod cuticles. The fine perpendicular canal-like elements present in the inter-laminae of many preparations we have examined are considered similar to the pore canals of extant arthropod cuticles, in that they are relatively narrow (about 1μ in diameter), are very numerous, and have been observed in all regions of the cuticle examined.

Organic material. The presence of brown organic material in trilobite cuticles has long been recognized. Davies (1894) considered it possibly to be a replacement product of the original organic material of the cuticle, Dalingwater (1973) isolated organic material from a trilobite cuticle after decalcification with E.D.T.A., and Teigler and Towe (1975) carried this study further by examining sections of the material with the TEM. Their observation of a delicate meshwork does not eliminate the possibility of the presence of laminae comparable with those of most extant arthropod cuticles, for their sections are apparently more or less horizontal and the pattern figured is not incompatible with the architecture observed in horizontal slices or breaks of extant cuticles (see Travis 1970; Dalingwater 1975). Further work is needed to establish the nature of this relict organic material and to determine its precise relationship with the inorganic component of the trilobite cuticle.

Subdivisions of the cuticle. In our description of the cuticle of *Asaphus raniceps* we define three zones based on the appearance and dimensions of their laminar units. The central and innermost zones apparently correspond with the median and inner subdivisions that Størmer (1930) defined in his classic study of the cuticle of *Tretaspis kiaeri*, although as previously noted (Dalingwater 1973) his pigmented layer is a dense micritic envelope. The term zone is deliberately used in this paper to avoid confusion with the layers of the trilobite cuticle recently defined mainly from light microscope observations (see text-fig. 2). The outer prismatic layer was not always present prior to etching (possibly removed with the overlying matrix), but when it was present at least part of it was etched back very rapidly in E.D.T.A., so the zones defined herein possibly all lie within the principal layer (the central and inner laminate zones certainly do). As the outer layer of the cuticle can show aspects other than prismatic (Teigler and Towe 1975), and as it is quite possible that this part of the cuticle may subsequently be shown also to contain laminae, at present we prefer to reserve judgement on the precise relationship of the outer prismatic layer and our outer laminate zone. Examination of newly formed cuticles may help to solve this problem and work is in progress on the material described by Miller *et al.* (1974).

We are confident that the trilobite cuticle described is similar to those of many extant arthropods in laminar organization and divisibility into zones based on



TEXT-FIG. 2. The major layers and laminate zones of the cuticle of *Asaphus raniceps*. *Right*: the previously defined layers (Dalingwater 1973). *Left*: the laminate zones defined in this paper.

laminar disposition. However, it is difficult to make any precise correlation of the trilobite zones and layers with those of any specific group of extant arthropods, for there is some variability in cuticular subdivisions between the different groups of extant arthropods, and the exact subdivision is based largely on histochemical criteria. Nevertheless, in being impregnated with mineral salts and in its general laminar organization, the trilobite cuticle described here most favourably resembles that of decapod crustaceans (e.g. *Austropotamobius pallipes*, see Pl. 10, fig. 4). We agree with Teigler and Towe (1975) that the trilobite cuticle is unusual in being so heavily impregnated with calcite, but suggest that this enables the production of a relatively very thick and strong cuticle, economic in terms of organic material. However, we would hesitate to attach any phylogenetic significance to this particular feature for other groups of crustaceans as well as the ostracods (e.g. cirripedes) have produced heavily calcitized cuticles in functional response to particular environmental demands. We must also add that in comparing the trilobite cuticle favourably with that of decapod crustaceans, we attach no phylogenetic significance to our analogy.

The epicuticle of many extant decapod crustaceans is calcified (Digby 1967; Welinder 1975) so it is quite possible that traces of a similar layer might be preserved in trilobites; the outermost layer described by Dalingwater (1973) is positionally and

structurally compatible with the extant decapod epicuticle. The prismatic layer and the outer laminate zone can be considered equivalent to the exocuticle, and the central zone to the calcified principal zone, of extant decapods. Comparison of the innermost zone of the trilobite cuticle described herein with the inner region of extant decapod cuticles presents a difficulty, for in the latter this is usually an uncalcified endocuticle refractory to fossilization. However, in some regions of, for example, crayfish cuticle, the uncalcified endocuticle laterally transforms into a region which is calcified, strictly speaking therefore part of the calcified principal zone, but still distinguishable by the relative narrowness of its laminar units (Dr. J. Kennaugh, pers. comm.). A similar situation may exist in the trilobite cuticle. Further investigation of the inner region of the trilobite cuticle is necessary, particularly to determine if there are any differences between the cuticles of intaglios and exuviae. This could reveal whether there is any resorption of material prior to ecdysis.

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CALCIFIED *PLECTONEMA* (BLUE-GREEN ALGAE), A RECENT EXAMPLE OF *GIRVANELLA* FROM ALDABRA ATOLL

by ROBERT RIDING

ABSTRACT. *Girvanella*, not previously reported from rocks younger than Cretaceous, is described from the Recent. It occurs as the calcified sheath of the filamentous blue-green alga *Plectonema gloeophillum* Borzi in small freshwater pools on Aldabra Atoll in the Indian Ocean. The sheaths are heavily impregnated during the life of the alga by micrite grade crystals of magnesian calcite which make them hard and potentially fossilizable and which preserve the filaments as small calcareous tubes 4–10 μm in diameter. This confirms the view that *Girvanella* represents a filamentous blue-green alga preserved by the calcification of its sheath, and it extends the range of the genus from Cambrian to Recent. The consistent relatively thin-walled morphology of *Girvanella*-type impregnated sheaths contrasts with the thickly microsparite encrusted sheaths of blue-green algae in environments of CaCO_3 cementation. This suggests a greater degree of control of the calcification process in *Girvanella* and supports the concept of specificity for calcification in some blue-greens. *P. gloeophillum* is believed to be only one of a number of extant filamentous blue-greens whose calcified sheaths are referable to *Girvanella*. At present *Girvanella* is still most conveniently placed in the Porostromata, which should be regarded as a group of tubiform calcareous algae.

THE size and morphology of the microscopic tubiform fossil *Girvanella* Nicholson and Etheridge suggest that it is the calcified sheath of a filamentous blue-green alga (Pollock 1918; Riding 1972, 1975). Blue-greens are among the oldest known fossils and the similarities between very ancient and extant forms indicate that they are morphologically conservative organisms (Schopf 1968, p. 653). If *Girvanella* is indeed a blue-green alga then it is reasonable to expect that it has a modern representative. Yet although *Girvanella* is known to range from the Cambrian to Cretaceous it has not previously been recorded from the Cenozoic (Riding 1975). The purpose of this paper is to draw attention to a Recent example of *Girvanella* from the Indian Ocean atoll of Aldabra.

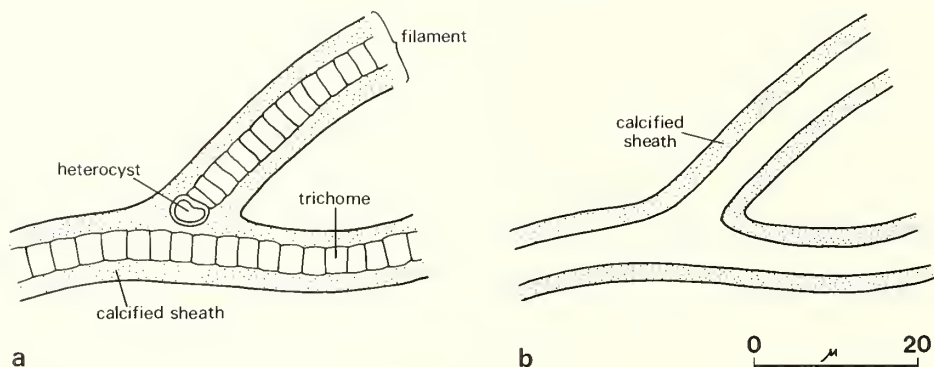
This living *Girvanella* is the small filamentous blue-green alga *Plectonema gloeophillum* Borzi. It inhabits freshwater pools on Aldabra and its sheath in these habitats sometimes becomes heavily impregnated during life by CaCO_3 which renders it hard and potentially fossilizable. The resulting simple sinuous calcareous tube is a small form of *Girvanella*. It seems likely that a variety of filamentous blue-greens from several families can, under suitable conditions, produce calcareous tubes referable to *Girvanella* or to related fossil genera. Thus, *P. gloeophillum* is thought to be only one of a number of extant blue-greens whose soft parts show them to be quite distinct taxa, but whose simple calcified sheaths can be bracketed together in the single fossil genus *Girvanella*.

CALCIFIED BLUE-GREEN ALGAE

Cyanophytes have a long geological record as calcified and silicified fossils and as algal stromatolites. Stromatolites are organosedimentary structures; they do not

readily reflect the types of organisms involved in their construction, which may include coccoid and filamentous bacteria and blue-green algae and also green algae. By contrast silicified fossil blue-greens can show remarkable preservation of the soft tissue, including details of cellular ultrastructure. Thus, stromatolitic and silicified blue-green algae represent extremes of preservation. They also differ markedly in abundance, stromatolites being relatively common whereas silicified microfloras are rather rare.

Calcified blue-green algae are intermediate between stromatolitic and silicified forms in the degree of morphological detail which they retain, and probably also in their over-all abundance through geological time. In the discussion of calcification (see below) it will be necessary to distinguish between calcification of the sheath on the one hand and massive encrustation of the filament on the other, both being types of calcification. But in *Plectonema* and *Girvanella* we are only dealing with the former. Calcification in this case only affects the mucilaginous sheath enclosing the strands of cells (trichomes). It takes place while the alga is living. Because CaCO_3 is incorporated into the sheath rather than into the cell walls of the alga only the external morphology of the algal filament is preserved and most of the features which are significant for the taxonomy of Recent blue-greens are lost (text-fig. 1). Filamentous

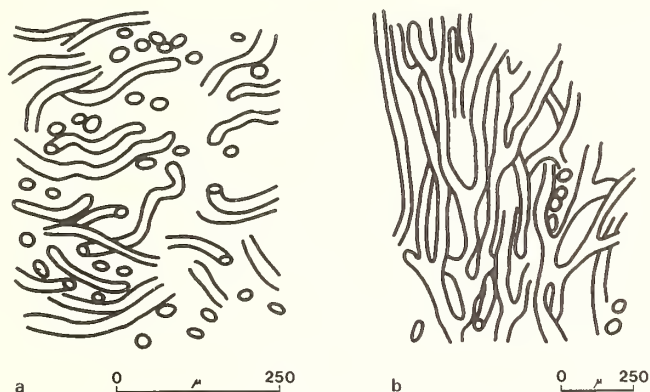


TEXT-FIG. 1. Post-mortem loss of morphological detail in calcified filamentous blue-green algae. The alga shown is *Tolypothrix*, a scytonematacean similar to *Plectonema* but possessing heterocysts. *a*, portion of living calcified filament. *b*, empty, potentially fossilizable, calcified sheath. Features observable in *a* but not in *b* include: presence of heterocyst, type of branching (false), number (one) and size of trichomes. The sections are longitudinal.

blue-green algae calcified in this way produce microscopic, morphologically simple, non-septate tubiform skeletons which may exhibit branching but which show few other distinctive characters. The relatively large diameters of these calcareous tubes and their lack of septa clearly distinguish them from the rather small trichomes of blue-green algae which are strands of cells. The expectation by some previous workers that fossil calcified blue-greens should reflect the form of the trichomes, and so be very small and septate, has tended to hinder recognition of the cyanophyte origin of the larger, non-septate calcified sheaths.

Nevertheless, Pia (1927, pp. 37-40) realized the true affinities of several of these small fossils but, being unable to relate them directly to Recent blue-green taxa, he

erected the group Porostromata to contain them. Not all of the genera originally included by Pia in the Porostromata appear to be blue-greens, but two of them, *Girvanella* and *Ortonella* Garwood (text-fig. 2), are regarded here as definitely having this affinity. Johnson's (1961, pp. 96-99) removal of several porostromate genera to the green Codiales was unwarranted (Riding 1975) and has subsequently confused the identity of fossil calcified filamentous blue-green algae. Much earlier Pollock (1918) had already made the suggestion, which is confirmed here, that *Girvanella* is a calcified cyanophyte sheath.



TEXT-FIG. 2. Morphology and orientation of *a*, *Girvanella*, and *b*, *Ortonella*, from photomicrographs of the type-specimens in Nicholson and Etheridge 1878, pl. 9, fig. 24; and Garwood 1914, pl. 20, fig. 2. *Girvanella* is flexuous, prostrate, and generally unbranched. *Ortonella* is straight, erect, and dichotomously branched. These contrasting features were used by Pia (1927) to separate the Porostromata into the Agathidia and Thamnidia respectively.

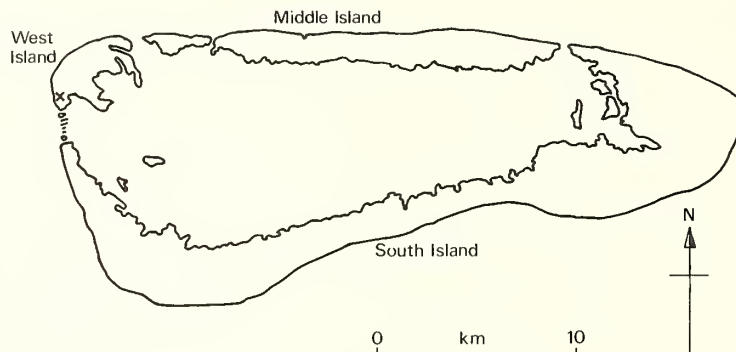
While it is unlikely that fossil calcified blue-greens can be referred to *single* extant genera it should be possible to discern closer relationships between fossil and living forms than are expressed by current palaeontological classifications and hence to improve our understanding of the nature and environmental significance of fossil calcified blue-green algae. I have suggested that the existence of Recent *Girvanella* is to be expected (Riding 1972) and that representatives are most likely to be found among filamentous blue-green families such as the Oscillatoriaceae, Rivulariaceae, Scytonemataceae, and Stigonemataceae (Riding 1975). The small Recent scytonematacean *P. gloeophilum* provides one such example of living *Girvanella*.

CALCIFIED *PLECTONEMA* FROM ALDABRA

Habitat. *P. gloeophilum* occurs in small freshwater pools on West Island, Aldabra; an atoll in the western Indian Ocean, 1200 km WSW. of the Seychelles. Aldabra receives an annual rainfall of approximately 1000 mm (D. R. Stoddart, pers. comm.). The freshwater pools, classed as 'temporary rainwater rockholes' by McKenzie (1971) are mostly very small, with volumes usually less than 3 m³. Their water chemistry and algal flora have been studied by Donaldson and Whitton (1976*a, b*). The pools provide water for tortoises, birds, crabs, and other animals and tend to become contaminated by excreta which produce

high concentrations of phosphate and ammonia. There is locally also some sea-water contamination of the pools, but they are essentially fresh. The pools support a varied algal flora with filamentous blue-greens such as *Calothrix*, *Oscillatoria*, *Phormidium*, and *Plectonema* usually present (Donaldson and Whitton 1976b). The locations of Aldabran pools are described by Donaldson and Whitton (unpublished).

The specimens of *Plectonema* described here were collected by Alan Donaldson from adjacent pools W7 and W127 on West Island (text-fig. 3) and he has kindly supplied the following details of their occurrence. These pools have volumes of approximately 1.8 and 0.3 m³ respectively. *Plectonema* forms mats on



TEXT-FIG. 3. Location (X) of adjacent *Plectonema*-containing pools W7 and W127 on West Island, Aldabra.

lime mud and silt flooring the pools. Collection of gas bubbles within the mats lifts them from the sediment and they rise to the surface to form dense globular flocs approximately 1 cm in diameter which are pale pink in colour and heavily calcified. In pool W7 from January to June 1973 *Plectonema* was associated with a wide variety of unicellular and filamentous green and blue-green algae. The following parameters of the pool-water were recorded by Donaldson during this period:

mean Ca concentration: 72.1 mg l⁻¹
 mean Mg concentration: 18.8 mg l⁻¹
 pH: 7.5–8.6
 temperature: 25.3–36.7 °C.

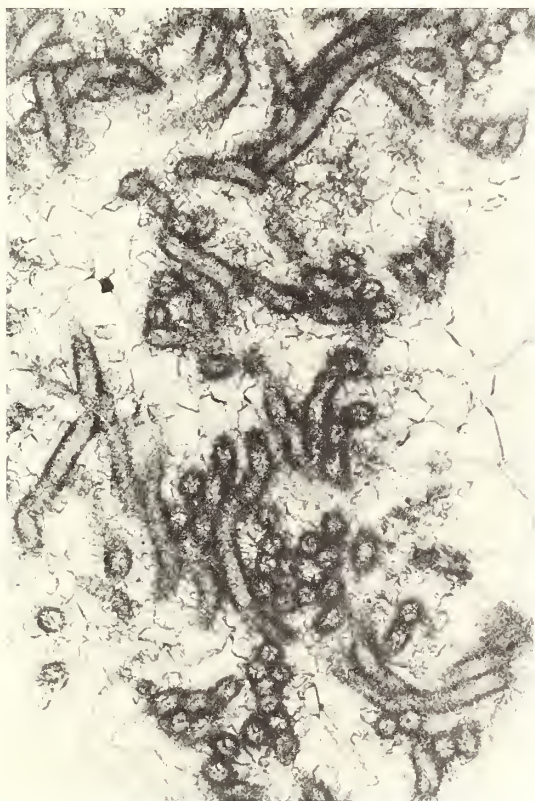
No measurements were made of pool W127 situated some 50 m north of pool W7. In April 1973 pool W127 contained a virtual uniculture of *P. gloeophilum* with abundant calcified flocs, samples of which are described and illustrated here.

Methods. The samples of *Plectonema* were air-dried in the shade following collection. For atomic absorption spectrophotometry small specimens were dissolved in 20% HCl. The insoluble residue constituted less than 5% by weight of the specimen. Mineralogy was determined by X-ray diffractometry. For scanning electron microscopy specimens were fractured and coated with carbon and gold. The photographs were taken on a Cambridge Stereoscan Mark II instrument operating at 20 kV.

Description. *P. gloeophilum* is a small, filamentous blue-green which shows false-branching and is non-heterocystous. The sheath is generally thin and contains a single trichome. The entire filament is 4–10 µm in diameter, and the sheath is up to 3 µm in thickness. Calcified sheaths of this species from pool W127 are figured in Plate 11. They form dense tangled masses of sinuous macaroni-like tubes. The CaCO₃ occurs as bladed and acicular micrite crystals 1–3 µm in size which form tufted clusters crudely orientated normal to the surface of the filament giving it a test-tube brush appearance. These crystals are calcite containing 4.6 mole % MgCO₃ and thus are close to the 4 mole % division between low- and high-magnesian calcite. Traces of the sheaths occur as patches and strands on the surfaces of the calcified tubes in the SEM. Biological preparations of the material show the calcite crystals to be contained within or very close to the surface of the sheath. Drying of the sheath in air, and in vacuum during preparation for electron

microscopy, causes it to shrink and exposes the crystals which then form very irregular inner and outer surfaces to the tube. The calcified tubes are approximately $6\text{ }\mu\text{m}$ in external diameter and $2\text{ }\mu\text{m}$ in the thickness of their walls. They exceed $140\text{ }\mu\text{m}$ in length and do not taper.

Comparison with Girvanella. *Girvanella* is a small, flexuous, rarely branching, tubiform fossil with a microgranular (micritic) calcareous wall (text-fig. 4). Specimens



TEXT-FIG. 4. *Girvanella* sp., from the Upper Devonian (Frasnian), Mount Hawk Formation, Mount Haultain, Alberta. Note constancy of tube diameter and relatively thin wall. Thin section courtesy of E. W. Mountjoy (McGill University); $\times 125$.

with external tube diameters from 1 to $100\text{ }\mu\text{m}$ are recorded in the literature. Whether the larger sizes really represent *Girvanella* is open to question but certainly the genus exhibits a large size range. Most specimens recorded have diameters in the range 8 – $30\text{ }\mu\text{m}$. For each specimen the tube diameter is constant and the total wall thickness is approximately 50% of the external diameter. *Girvanella* occurs encrusting grains or as small discrete masses which are themselves grains. Whether the latter are fragments or are original unbroken masses of filaments is not usually clear.

The similarity between *Girvanella* and the calcified *Plectonema* sheaths described here is striking. The ratio of wall thickness to tube diameter in *Plectonema* (2:3)

somewhat exceeds that in *Girvanella* (approximately 1:2) and the surface of the tube is more irregular, but it is likely that both these features would be reduced during diagenesis. Otherwise there are no observable differences between *Girvanella* and these specimens of *Plectonema*.

OTHER CALCIFIED ALGAL FILAMENTS

Although this is the first specific report of Recent *Girvanella*, calcified algal filaments have previously been noted in several studies of Recent intertidal and supratidal algal mats from the Bahamas. Black (1933, p. 170, pl. 22, fig. 28) first noted that the supratidal algal mats of the interior of Andros Island tend to be calcified. Monty (1967, p. B67, pl. 6) compared calcified filaments of *Scytonema myochrous* from the supratidal of eastern Andros with *Ortonella*. These specimens of *Scytonema* are erect and dichotomously branched and are approximately 20 μm in external diameter. Calcified *Scytonema* filaments have also been figured from the supratidal of north-western Andros by Shinn *et al.* (1969, fig. 12*b*) but these specimens are less upright in appearance and resemble *Girvanella* more than *Ortonella*. Similar tubules have been described from calcareous crusts in late Pleistocene limestones of Barbados (James 1972, fig. 6*d*). They are 15–20 μm in external diameter with a wall thickness of approximately 5 μm and are composed mainly of equant calcite crystals 1.5–2.5 μm in size (James 1972, p. 826). James compared them with filaments of the extant blue-green alga *Schizothrix* and attributed them to 'blue-green algae or possibly root-hairs'. They closely resemble the calcified *Plectonema* sheaths from Aldabra in morphology, but they are larger.

Calcite encrusted cyanophyte filaments which are rather different from those described here have been reported from freshwater stream tufa in south-western Germany (Irion and Müller 1968). The filaments belong to Recent oscillatoriacean blue-greens 'with a diameter of 5 μm ; they are encrusted by isometric crystals with a rounded surface. The average diameter of the crystals is 15 μm ' (Irion and Müller 1968, p. 165). Apparently the crystals form a thick crust *on*, rather than *within*, the sheath. The specimens are not figured but it can be inferred that they would be tubes with diameters of at least 35 μm . Their thick walls (more than 85% of the tube diameter) and microsparite grade crystals distinguish them from *Girvanella* and *Plectonema* tubes.

EXPLANATION OF PLATE 11

Scanning electron micrographs of calcified sheaths of *Plectonema gloeophilum* Borzi from freshwater pool W7, West Island, Aldabra.

Fig. 1. Tangled 'ball of knitting wool' appearance of mass of tubes, $\times 220$.

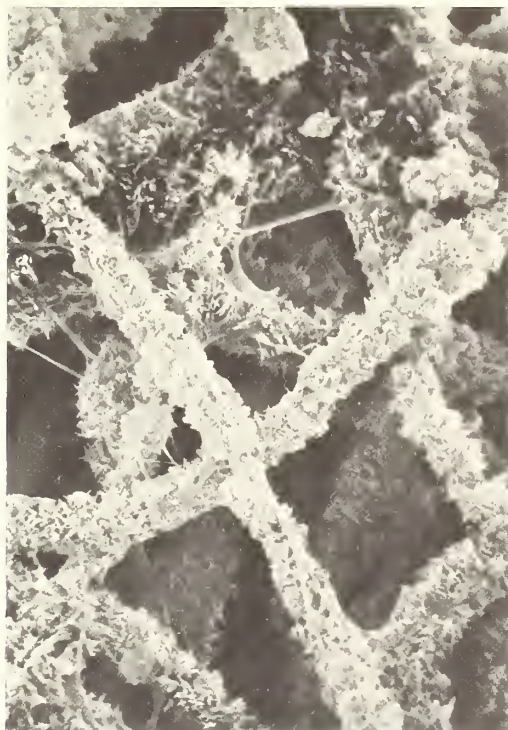
Fig. 2. Detail of Fig. 1 showing unbranched, uniform diameter sheaths associated with thin dried strands of mucilage. Large uncalcified filament in the upper part of the photograph is probably the green alga *Oedogonium*, $\times 1100$.

Fig. 3. Surface of calcified filament showing bladed and acicular micrite grade crystals of magnesian calcite. Note general orientation of crystals normal to sheath surface, and traces of dried mucilage, $\times 5500$.

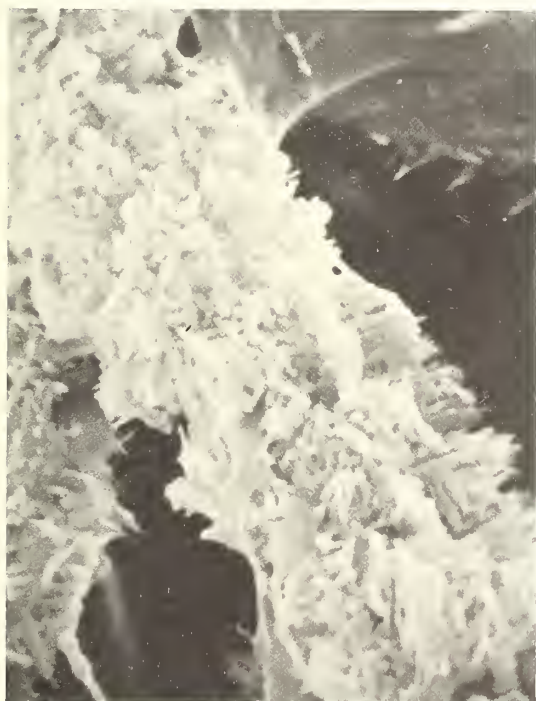
Fig. 4. Fracture (or termination) of filament showing relatively thin wall and hollow interior, $\times 5400$.



1



2



3



4

RIDING, calcified *Plectonema*

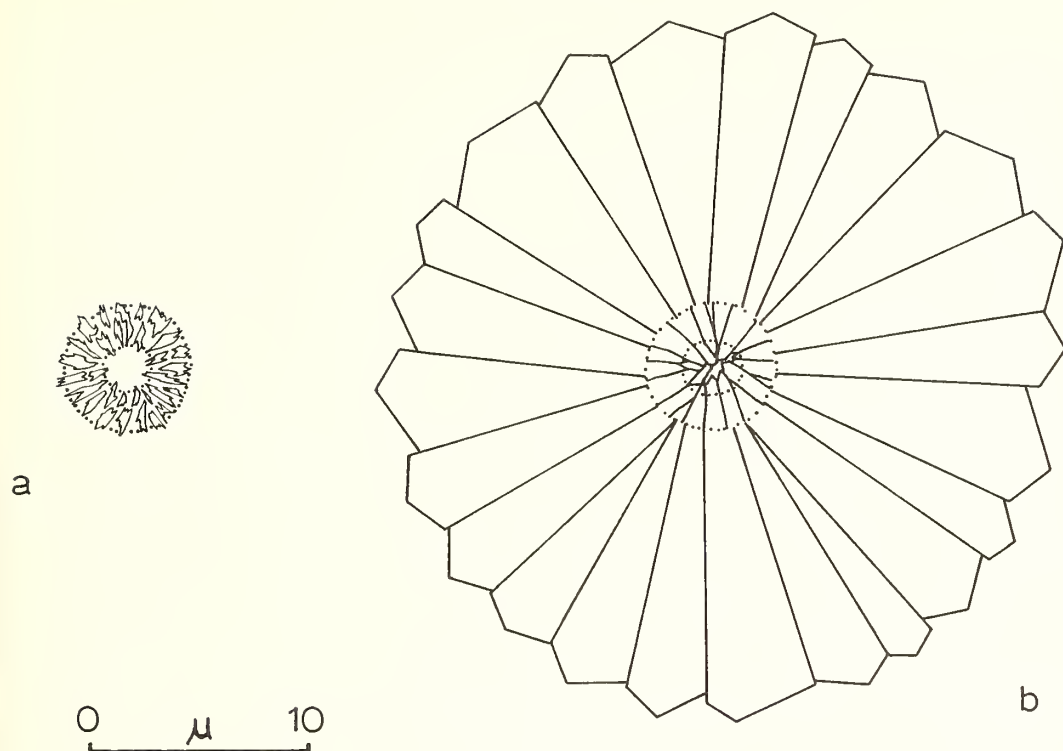
There are relatively few records of Recent calcified blue-green filaments from subtidal marine environments. Winland and Matthews (1974, fig. 3c) figure calcified sheath material associated with grapestone from Great Bahama Bank. The form of the filament is not shown but it has a diameter of 10–12 μm and a sheath thickness of approximately 2 μm . The CaCO_3 crystals are 1–2 μm in size and have rhombic and acicular forms. These sizes and shapes are similar to those of the crystals in *Plectonema* from Aldabra. A circular structure, which may be a cross-section of a similar filament, has been figured from Recent Red Sea reefs (Friedman *et al.* 1974, fig. 15), although it could also be a pellet. It is 9 μm in diameter with a wall thickness of 3 μm and consists of high-magnesian calcite. Calcified filaments of the green alga *Ostreobium* have been described from Recent Bermudan cup reefs (Schroeder 1972). This endolithic alga has a diameter of 2–20 μm . The principal morphological difference between *Ostreobium* and blue-green algal filaments is the local swellings shown by the green alga. *Ostreobium* is not normally calcified but in small internal cavities in the cup reefs it has become encrusted by equant, bladed, or fibrous crystals of high-magnesian calcite during early subsea cementation. The calcite crystals also encrust adjacent non-algal surfaces. The crystals are relatively large with widths of 5 μm and lengths of 10–20 μm being common. Not only are the *Ostreobium* filaments externally encrusted but, following decay of the alga, the remaining cavity is also infilled by calcite crystals. Hence the filaments are preserved by thick external crusts plus internal cores. The core is up to 20 μm in diameter and the crust is up to 150 μm in thickness (Schroeder 1972, p. 20). Thus, the total diameter of the calcified filament ranges from 15 to 300 μm or more, and it is ultimately preserved as a rod rather than as a tube. Heavily encrusted filaments of this type resemble those of blue-green algae from freshwater streams and tufa deposits.

D. R. Kobluk and M. J. Risk inform me that they have seen calcification of *Ostreobium* filaments projecting from experimentally introduced Iceland spar crystals in a shallow subtidal environment at Jamaica. Micrite and microspar low-magnesian calcite crystals coat the inner and outer surfaces of exposed dead filaments and give rise to thickly encrusted rods 8–30 μm in diameter comparable with those described by Schroeder.

DISCUSSION

There are two distinct types of calcified blue-green algal filament: micrite-impregnated sheaths and microspar-encrusted sheaths (text-fig. 5). Calcified Aldabran *Plectonema*, and by analogy fossil *Girvanella*, represent impregnated sheaths without significant external encrustation. The Bahaman filaments described above from both the supratidal (Black 1933; Monty 1967; Shinn *et al.* 1969) and subtidal (Winland and Matthews 1974) fall within the same category. In contrast blue-green filaments in freshwater tufa (Irion and Müller 1968) are thickly encrusted, as are subtidal cemented green algal filaments (Schroeder 1972).

Any heavily encrusted filaments recorded as fossils should be distinguishable from *Girvanella* and *Ortonella* tubes in being wider, having greater wall thickness, being composed of coarser crystals, showing variability in diameter within a single specimen, and in some cases by being infilled by additional cement to form a rod. These



TEXT-FIG. 5. *a*, micrite impregnated, and *b*, microspar encrusted sheaths in diagrammatic cross-section. The consistent thin-walled morphology of *Girvanella* (type *a* sheath) throughout its geological history indicates that *a* and *b* do not simply represent different stages of the same process but that different mechanisms of calcification are involved: 'controlled' (essentially biochemical) in *a*, 'uncontrolled' (essentially physicochemical) in *b*.

contrasts between thickly encrusted sheaths and impregnated sheaths suggest that at least the *rate* of the calcification process is operating differently in the two cases, but there is also circumstantial evidence which suggests that the *type* of process differs as well.

Calcification. It has gradually become clear that calcification processes operate quite differently in different algal groups (see Arnott and Pautard 1970) and are to some extent reflected by the site of CaCO_3 deposition on or within the plant. In the red Corallinaceae the site of calcification is the cell wall; in the green Codiales and Dasycladales it is mainly extracellular but the calcareous skeleton forms an intimate part of the plant body. In Aldabran *Plectonema*, and apparently in calcified blue-greens generally, calcification is entirely extracellular, being restricted to the mucilaginous external sheath. This suggests a mechanism which is not entirely under the control of the plant's metabolism and is supported by the variable occurrence of calcification in the group since no blue-green species is known to be always calcified. It is tempting to go on to hypothesize an essentially physicochemical precipitation mechanism in calcified blue-greens, even though this is not applicable

to any other calcareous algae, and two supporting lines of evidence can be derived from Aldabran *Plectonema*.

(i) *Environment of occurrence*. CaCO_3 precipitation due to photosynthetic utilization of CO_2 will be limited in normal marine environments by the buffering capacity of sea-water, but this regulation will not operate in fresh water where removal of CO_2 species can readily cause precipitation. The relatively high temperature, pH, and calcium concentration of the Aldabran pools containing calcified *Plectonema* are conditions favouring CaCO_3 precipitation and removal of CO_2 from the system during algal photosynthesis could provide the final stimulus for this process.

(ii) *Nature of the CaCO_3* . Three features of the *Plectonema* skeletons described here are 1, calcite mineralogy; 2, micrite-grade crystal size; and 3, incorporation of magnesium. Calcite formation is inhibited in sea-water by abundance of magnesium cations but it is the normal phase to be precipitated in fresh water. The Mg content of the calcite indicated by the AAS analyses is probably an over-estimate because it will include magnesium from the organic sheath material (see Gebelein and Hoffman 1971) due to the acid preparation method used. Even so it is only low in the high-magnesian calcite range and can be seen as a reflection of the magnesium content of the pool-water. The small size of the calcite crystals is probably due to a rapid crystallization rate. Thus, the mineralogy, composition, and texture of the CaCO_3 in these algal sheaths are consistent with their meteoric, surficial environment of formation (see Folk 1974, fig. 5). This conformity with normal physicochemical controls of carbonate mineral formation is another indication that biological involvement in the precipitation process could be limited.

There are, however, two significant features of blue-green calcification which raise doubts about a simple physicochemical mechanism.

(i) Calcification in blue-greens is variable but it does not appear to be wholly controlled by the environment since certain species seem to be more predisposed to calcification than others. This specificity for CaCO_3 deposition is suggested by studies reported by Golubić (1973, p. 436) and is supported by the mutual occurrence of calcified and uncalcified blue-green species.

(ii) If *Girvanella* were primarily dependent upon cementation processes for its skeletogenesis then its wall thickness could be expected to vary greatly according to the degree of precipitation proceeding in the micro-environment of a particular specimen. It should be capable of greatly exceeding the 50% of the tube diameter characteristic of the genus. Furthermore its tubiform morphology should be modified, in some cases at least, by infilling by a cement core as in *Ostreobium* reported by Schroeder and others. Yet thick microsparite-walled *Girvanella*-type fossils and similar rod-shaped forms are conspicuous by their absence from the geological record of the past 600 ma. This morphological discontinuity between *Plectonema*/*Girvanella* tubes (impregnated sheaths) and encrusted sheaths suggests that the former are produced by blue-green algae which have the capacity to control calcification and are not simply dependent upon an external physicochemical process.

Accordingly it is reasonable to postulate a distinction not only between the degree of calcification, i.e. between impregnated and encrusted sheaths, but also a corresponding distinction in the control (and timing) of calcification, i.e. between essentially *controlled* and *uncontrolled* calcification in blue-green algae. In forms such as

Girvanella and *Ortonella* and their Recent analogues I suggest that the alga exerts a controlling influence over calcification and promotes crystal deposition in the sheath but not beyond it. The skeleton is thus a relatively thin-walled tube formed during the life of the alga. In other calcified forms known from freshwater tufa deposits and from Recent environments of subsea cementation calcification is beyond (or extends beyond) the control of the plant and results in gratuitous deposition of CaCO_3 either during life or post-mortem. These skeletons are relatively thick-walled tubes or rods.

Thus, while several features of CaCO_3 deposition in blue-greens are consistent with an essentially physicochemical control photosynthetically triggered by an otherwise passive alga, the morphology of *Girvanella* and its Recent analogues together with the mutual occurrence of calcified and uncalcified forms support the concept of specificity for, and control of, calcification in some blue-greens. The degree of control is clearly not complete since a species which calcifies in one habitat will not necessarily calcify elsewhere. Yet it is of interest that even the relatively unsophisticated blue-greens could have a control over their calcification which might be as distinctive, if less refined, as those operating in green, yellow-green, and red algae. But the nature of this calcification mechanism in blue-greens has still to be elucidated.

Taxonomic significance. The specimens of *Plectonema* from Aldabra and those of *Scytonema* described by Monty (1967) provide Recent analogues of *Girvanella* and *Ortonella* respectively. Is *Girvanella* really *Plectonema*, or the other way round? The answer is neither. The amount of morphological detail preserved by *Girvanella* and *Ortonella* is so limited (text-fig. 1) that it could relate to a wide variety of extant filamentous blue-greens (Riding 1975). It is likely that both *Girvanella* and *Ortonella* represent a number of Recent biological taxa, of which *Plectonema* and *Scytonema* are only two. Thus, *Plectonema* is represented by the entire alga, trichomes as well as sheath. But its calcified sheath when the soft parts have been removed is *Girvanella*. *Girvanella*, on the other hand, is a calcified blue-green algal sheath devoid of soft parts. It is only distinguished from other calcified sheaths by its generally unbranched, sinuous morphology, constant diameter, and prostrate habit. In contrast, *Ortonella* is erect with subparallel filaments and dichotomously branched (text-fig. 2).

This distinction between *Girvanella* and *Ortonella* is very crude when compared with the probable multiplicity of biological taxa merged within them, but it is possible that some environmental information can be gleaned from their gross differences in external morphology to compensate somewhat for the loss of detail in soft-part structure. Rather than merely representing a variety of taxa they might represent groups of morphologically similar ecophenes (environmental growth forms) of a variety of taxa. The distinction between erect and prostrate form seen in *Ortonella* and *Girvanella* extends to a number of porostromate genera and was recognized by Pia (1927, pp. 37–40) when he subdivided the Porostromata into the Agathidia (prostrate forms such as *Girvanella* and *Sphaerocodium*) and Thamnidia (erect forms such as *Hedströmia*, *Mitcheldeania*, and *Ortonella*). The erect, tufted habit of the Thamnidia suggests phototropic growth possibly induced by physical confinement, while the prostrate habit of the Agathidia suggests higher

light availability. But caution should be exercised in these interpretations and a genetic, as opposed to environmental, control of these forms cannot be excluded (B. A. Whitton, pers. comm.).

Pia intended the Porostromata to contain calcareous tubiform fossils which he believed to be blue-green algae but which he was unable to place in extant groups. In practice the affinities of genera normally included in the Porostromata have been in doubt and attempts to use the group as a 'Section' of the Schizophyta (bacteria and blue-green algae) have not been very successful (see Johnson 1961, p. 194). Instead the Porostromata have been most useful not as a group of fossil calcareous blue-green algae but as a group of small tubiform fossils. In my view this is still the case and will remain so until the affinities of more members of the group can be clarified. It would be premature to assume that because there is now good evidence that two genera, *Girvanella* and *Ortonella*, are the calcified sheaths of filamentous blue-greens that this confirms Pia's view of the group as a whole. It is still possible that calcified green algae are represented by some of the porostromate genera, especially those with relatively large tubes, and an apparent transition from Porostromata with closely appressed tubes to members of the Solenoporaceae remains to be clarified. Neither would it be advantageous at present to remove *Girvanella* and *Ortonella* from the Porostromata and place them in extant blue-green families because of the probability that they represent forms from several families. The members of the Porostromata form a reasonably homogeneous morphological group characterized by their microscopic, calcareous, non-septate, tubiform skeletons. It should be retained as a group of algae rather than blue-green algae. The following genera can be included: *Bevocastria* Garwood, *Cayeuxia* Frollo, *Girvanella*, *Hedströmia* Rothpletz, *Mitcheldeania* Wethered/Garwoodia Wood, *Ortonella*, *Sphaerocodium* Rothpletz. *Epiphyton* Bornemann, originally included by Pia, is not tubiform, and *Otonosia* Twenhofel and *Somphospongia* Beede, included in the group by Johnson (1961, pp. 195–196) are aggregates of porostromate tubes, not tubiform fossils themselves.

CONCLUSIONS

1. Calcified *P. gloeophyllum* in freshwater pools on Aldabra is a Recent analogue of *Girvanella*. It is a 'living fossil' in the sense that *Girvanella*, while known to range from Cambrian to Cretaceous, was previously unrecorded from Cenozoic rocks. This discovery confirms previous suggestions that *Girvanella* represents the calcified sheaths of filamentous blue-green algae (Pollock 1918; Riding 1972, 1975) rather than being a calcified green alga (Frémy and Dangeard 1935; Johnson 1963, p. 26).

2. In fresh water and marine environments where CaCO_3 cementation is common, small algal filaments can become thickly encrusted by microspar. Limitation of calcification to the sheath in *Plectonema* and *Girvanella* produces a quite different, consistently thin-walled, tubiform micritic skeleton suggesting that precipitation of the crystals does not proceed uncontrolled in this case. This supports the idea that certain blue-greens have a specific capacity for calcification. However, the fact that *Plectonema* is not always calcified indicates that control of calcification by the alga

is partial, rather than complete, and is presumably dependent on some overriding environmental factors.

3. The morphological discontinuity between calcified sheaths and encrusted filaments, together with differences in their environment of occurrence, support a distinction between relatively controlled and relatively uncontrolled calcification in blue-greens. Controlled calcification can proceed in a variety of carbonate environments, not only those where cementation and tufa-formation are general, and occurs in living algae. Micrite crystals impregnate the sheath but do not significantly encrust its external surface. In this way the size and form of the sheath are preserved. Uncontrolled calcification only takes place in environments of cementation and tufa-formation and can occur during life or post-mortem. Filaments are encrusted by microspar or larger crystals to form a thick-walled tube which only grossly reflects the original morphology of the alga. The interior of the tube may be infilled to produce a solid rod of CaCO_3 . Controlled and uncontrolled calcification seem to reflect contrasting mechanisms of CaCO_3 deposition, the former essentially biochemical, the latter essentially physicochemical.

4. *Girvanella* probably includes various filamentous blue-green algae and not solely fossil *Plectonema*. Consequently, the Porostromata remains the most suitable higher taxon in which *Girvanella* can be placed at present. The Porostromata includes some blue-green genera, but also others whose precise affinities remain uncertain. It should be regarded as primarily a morphological group of algae.

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SIGNIFICANCE OF COILED PROTOCOLORALLA IN SOME MISSISSIPPIAN HORN CORALS

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ABSTRACT. Planispirally coiled protocoralla are described in *Cyathaxonia tantilla* (Miller) from the Lower Mississippian (Lower Carboniferous) of the western United States, the first record of this phenomenon in corals. Coiling is interpreted as a mode of attachment of young coralla to planktonic algae. The postulated pseudoplanktonic growth habit may be a significant factor in the widespread distribution of this species and other species of *Cyathaxonia*, which are generally found in rocks that record a bottom environment considered unfavourable for optimum coral growth.

SPECIMENS of horn corals with perfectly preserved tips are rarely observed in compact Palaeozoic limestones, even though corals are abundant in these rocks. Freeing of silicified specimens from limestone matrix by dissolving the matrix in acid often provides unusual opportunities to observe the earliest growth stages of these corals. This report presents the results of a study of approximately 500 etched silicified specimens of *Cyathaxonia tantilla* (Miller) from the Paine Member of the Lodgepole Limestone (Lower Mississippian, Kinderhookian, lower Tournaisian) collected from seven localities in the western United States (Utah and Montana). At Brazer Canyon, Utah, samples collected from closely spaced intervals through the lower part of the Lodgepole Limestone provided an unusual opportunity to study morphological variation in the earliest stage of these small horn corals. The Brazer Canyon material revealed a planispirally coiled protocorallum never before reported in corals. Discovery of the same phenomenon in specimens from four other localities suggests that a coiled brephic stage was a common feature of *C. tantilla*.

NATURE AND SIGNIFICANCE OF THE BREPHIC STAGE

Nature of samples. The material from Brazer Canyon was collected from 0·3 m intervals through the lower 14·4 m of the Lodgepole Limestone and from 15·6 m and 18·7 m above the base. Three hundred and twenty specimens of *C. tantilla* in which all or part of the brephic stage (0–6 septa) is preserved were isolated for analysis from the Brazer Canyon samples (Table 1). In the overwhelming majority of these specimens (288), no evidence of attachment was observed. In most specimens, the tip was broken off (Pl. 12, fig. 7); in some, the tip is preserved, but abraded (Pl. 12, fig. 4). Perfect specimens are in two categories: (1) coiled tip (25 specimens) (Pl. 12, figs. 11–18), and (2) tip with lateral or basal attachment scar (7 specimens) (Pl. 12, figs. 9, 10). Coiled tips are present throughout almost the full stratigraphic range of the species (Table 1). Perfect tips are similarly rare in samples of *C. tantilla* from other localities in Montana and Utah (Table 2). Thus, out of approximately 500 specimens studied, all or part of the brephic stage is preserved in 348, but

breakage or abrasion of the tip prevents determination of the nature of attachment in all but 38 specimens, of which 30 have coiled tips and 8 have lateral or basal scars of attachment.

TABLE 1. Nature of protocorallum in 320 specimens of *Cyathaxonia tantilla* (Miller) from Brazer Canyon section, Utah.

Metres above base of Lodgepole Limestone	USGS Upper Palaeozoic locality number	Number of specimens with preserved brepheic stage			Total
		Coiled tips	Lateral attachment	No evidence of attachment	
0-0.6	16801-PC, 16802-PC	8	3	59	70
0.6-1.2	16803-PC, 16804-PC	9	2	119	130
1.2-1.8	16805-PC	2	0	18	20
1.8-2.4	16806-PC, 16807-PC	0	0	0	0
2.4-3.0	16808-PC, 16809-PC	1	0	11	12
3.0-3.6	16810-PC	0	0	2	2
3.6-4.2	16811-PC	1	0	2	3
4.2-4.8	16812-PC	0	0	1	1
4.8-5.4	16813-PC	0	0	2	2
5.4-6.0	16814-PC	0	0	0	0
6.0-6.6	16815-PC	0	0	5	5
6.6-7.2	16816-PC	1	0	1	2
7.2-7.8	16817-PC	0	0	1	1
7.8-8.4	16818-PC	0	0	5	5
8.4-9.0	16819-PC	0	0	0	0
9.0-9.6	16820-PC	0	0	3	3
9.6-10.2	16821-PC, 16822-PC	0	0	3	3
10.2-10.8	16823-PC, 16824-PC	0	0	1	1
10.8-11.4	16825-PC	0	1	4	5
11.4-12.0	16826-PC	1	0	3	4
12.0-12.6	16827-PC	0	1	27	28
12.6-13.2	16828-PC	2	0	14	16
13.2-13.8	16829-PC	0	0	6	6
13.8-14.4	16830-PC	0	0	0	0
15-6	16831-PC	0	0	1	1
18-7	16832-PC	0	0	0	0
	Totals	25	7	288	320

TABLE 2. Nature of protocorallum in specimens of *Cyathaxonia tantilla* (Miller) from localities in Montana and Utah other than Brazer Canyon.

Locality	USGS Upper Palaeozoic locality number	Number of specimens with preserved brepheic stage			Total
		Coiled tips	Lateral attachment	No evidence of attachment	
Logan, Montana	17356-PC	1	0	1	2
	17357-PC	0	0	4	4
White Peak, Montana	20164-PC	1	0	5	6
Squaw Creek, Montana	20600-PC	0	1	2	3
Sacajawea Peak, Montana	20641-PC	2	0	7	9
Emma Canyon, Utah	16911-PC	0	0	1	1
Baldy Mountain, Montana	17911-PC	1	0	1	2
	17913-PC	0	0	0	0
	17914-PC	0	0	0	0
	17915-PC	0	0	1	1
	Totals	5	1	22	28

Description of coiled tips. The brephic stage (protocorallum) is defined as the part of the corallum in which the first six septa (protosepta) appear. It is distinguished externally by the absence of the longitudinal septal grooves and interseptal ridges present in later growth stages (Pl. 12, figs. 12, 13). In the thirty specimens with coiled tips, the protocorallum ranges from 0.9 to 2.0 mm in length and has a mean length of 1.3 mm. In the lower half of the protocorallum, the corallum is evolutely coiled, ordinarily planispirally, to form a single 360° volution. The diameter of the coil ranges from 0.5 to 1.0 mm and has a mean value of 0.7 mm. The diameter of the corallum at the top of the volution ranges from 0.4 to 1.0 mm and has a mean value of 0.6 mm. The corallum is coiled about an open umbilicus which ranges from 0.05 to 0.30 mm in diameter and has a mean diameter of 0.13 mm.

Above the coil, the protocorallum may be erect (no change in direction of the corallum axis), geniculate (one or more changes in direction of the corallum axis in one plane), or vermiform (one or more changes in direction of the corallum axis in more than one plane). In the specimens studied, 47% are erect, 23% are geniculate, and 30% are vermiform. One or more protosepta were observed within the coiled part of the corallum in seven specimens.

Coiled tips are ordinarily observed in individuals that died in the neanic stage. The length of the corallum in specimens studied ranges from 1.9 to 14.2 mm, but the mean length is only 4.2 mm, and all but two specimens are 6.5 mm long or less. The maximum corallum diameter in these specimens ranges from 1.2 to 4.5 mm, but the mean diameter is 2.4 mm, and all but two specimens have a maximum diameter of 3.5 mm or less. The number of septa in the calice ranges from 6 to 34, but the mean is 22, and all but one specimen has 30 septa or less.

Interpretation. Most small, solitary, curved-conical rugose corals observed by the writer show basal or lateral attachment scars in young specimens in which the protocorallum is preserved, indicating that these corals ordinarily were fixed to some stable object on the substrate immediately after settling of the larvae. Attachment scars are not ordinarily seen on adult specimens of these corals; this suggests that the corallum subsequently broke loose from its attachment when its weight became too great for the cemented tip to support, and then lay on its side, changing its growth direction in order to maintain a position conducive to optimum feeding and growth. Evidence and theories bearing on the growth habits of such corals have been summarized by Sando (1961, pp. 75-79). Lateral or basal attachment scars were observed in 8 of the 38 specimens of *C. tantilla* having perfectly preserved tips, indicating that some of these corals followed the common growth pattern. The presence of a coiled tip and the lack of attachment scars in the other thirty specimens suggests that coiling about some linear object was the principal mode of fixation of the protocorallum. In order to coil about an object lying on the substrate, the polyp would have had to exert a lifting force or to submerge its feeding mechanism in the substrate; the object of attachment was therefore probably above the substrate. The only linear objects of diameter comparable with that of the umbilicus of the coiled tip found in the coral samples are productoid brachiopod spines (0.1-0.2 mm diameter) and the crossbars in fenestellid bryozoan zoaria (0.1-0.2 mm diameter). These are rejected as objects of attachment because none of the coralla were

found attached to them and because many of the coralla have an umbilicus of smaller diameter (0.05 mm) than the diameter of the postulated attachment objects.

The absence of attachment objects within the umbilici of the coiled tips suggests that the objects were composed of material that was not preserved. The filaments of modern marine algae are in the size range required (W. H. Adey, pers. comm. 1975), and marine algae are widely known from rocks of Mississippian age. However, the only possible algal remains known from the Paine Member of the Lodgepole Limestone are forms identified as *Calcisphaera*, *Vicinisphaera*, *Bisphaera*, and '*Radiosphaera*' (Mamet in Sando *et al.* 1969, p. E-13), which are thought to be planktonic algal cysts (B. L. Mamet, pers. comm. 1975). The associated benthonic fauna of foraminifers, corals, brachiopods, gastropods, bryozoans, and pelmatozoans consists of sparse, poorly diversified and depauperate forms adapted to an impoverished environment. The dark, thin-bedded, cherty, fine-grained, argillaceous, and silty beds of the Paine Member have been interpreted as sediments deposited in relatively deep, turbid water (Wilson 1969, pp. 15-16; Smith 1972, p. 31; Sando 1976), and as much as 50 m of relief has been measured on associated bioherms (Cotter 1965, p. 888). Thus, the weight of evidence favours an aphotic bottom environment for the Paine Member, which would preclude attachment of *Cyathaxonia tantilla* to benthonic algae.

EXPLANATION OF PLATE 12

All specimens are *Cyathaxonia tantilla* (Miller) from the Paine Member of the Lodgepole Limestone. All but fig. 5 are from Brazer Canyon, Utah.

Fig. 1. Transverse thin section, ephebic stage, USNM 222532b, USGS loc. 16803-PC, $\times 12$.

Fig. 2. Longitudinal thin section, ephebic stage, USNM 222530, USGS loc. 16803-PC, $\times 7$.

Figs. 3, 4. Counter and alar views, respectively, of etched ephebic corallum having abraded tip, USNM 222529, USGS loc. 16803-PC, $\times 2$.

Fig. 5. Alar view, etched ephebic corallum having coiled tip, USNM 222591, USGS loc. 20641-PC, Sacajawea Peak, Montana, $\times 2$.

Fig. 6. Broken tip of etched ephebic corallum showing 6 protosepta, USNM 222544, USGS loc. 16803-PC, $\times 10$.

Fig. 7. Broken tip of etched ephebic corallum showing initial axial septum, USNM 222520, USGS loc. 16801-PC, $\times 10$.

Fig. 8. Broken etched ephebic corallum showing tuberculated septa, USNM 222545, USGS loc. 16804-PC, $\times 5$.

Figs. 9, 10. Alar views of etched neanic coralla showing lateral and basal attachment scars. 9, USNM 222524, USGS loc. 16802-PC, $\times 10$. 10, USNM 222518, USGS loc. 16801-PC, $\times 10$.

Fig. 11. Alar view of etched neanic corallum having coiled tip, USNM 222516, USGS loc. 16801-PC, $\times 10$.

Figs. 12, 13. Alar and cardinal views, respectively, of etched neanic corallum having coiled tip, USNM 222514, USGS loc. 16801-PC, $\times 10$.

Fig. 14. Enlarged alar view of protocorallum of specimen shown in figs. 12 and 13, USNM 222514, USGS loc. 16801-PC, $\times 20$.

Fig. 15. Cardinal view of etched neanic corallum having coiled tip, USNM 222517, USGS loc. 16801-PC, $\times 10$.

Figs. 16, 17. Alar and tip views, respectively, of etched neanic corallum having broken coiled tip showing axial septum, USNM 222536, USGS loc. 16803-PC, $\times 10$.

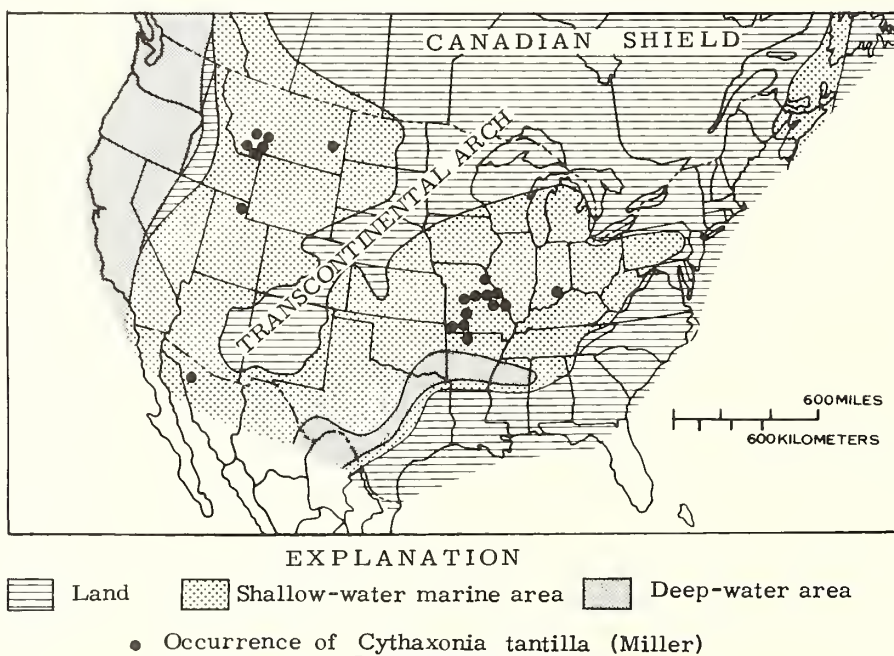
Figs. 18, 19. Alar and cardinal views, respectively, of etched neanic corallum having coiled tip, USNM 222515, USGS loc. 16801-PC, $\times 10$.



SANDO, Mississippian corals

The corals were probably attached to algae that were floating in the photic zone of the sea-water. The small size and consequent low mass of the young corallum is compatible with a planktonic habit. Prior to maturity, increased mass of the corallum may have caused most individuals to descend to the sea-floor, where they spent the remainder of their lives lying on their sides. These forms produced a curved corallum in response to the need for maintaining their oral surfaces in an optimum feeding position (Pl. 12, fig. 14). Ordinarily the delicate coiled protocorallum was destroyed on the sea-floor either by other organisms (see Sando 1961, p. 79) or by mechanical abrasion while the corallum was still occupied by the living polyp or after death. Some individuals (Pl. 12, fig. 5) either survived such destructive influences or remained attached to floating aggregates of algae throughout growth. The straight-conical rather than curved-conical form of the few mature specimens that show coiled tips suggests a pseudoplanktonic habit throughout growth for these individuals. Other individuals having basal or lateral attachment scars evidently were attached to objects on the substrate and were sessile throughout post-larval growth.

Significance. The postulated pseudoplanktonic growth habit of the specimens studied has an important bearing on the migration potential of *Cyathaxonia*. Inasmuch as specimens with perfectly preserved tips are extremely rare, this growth habit may have been a common feature of *C. tantilla* and perhaps other species of the genus. *C. tantilla* occurs in strata of middle and late Kinderhookian and earliest Osagean age in both the western and eastern United States (text-fig. 1) despite a



TEXT-FIG. 1. Palaeogeographical map of the United States and adjacent areas during Kinderhookian time, showing occurrences of *Cyathaxonia tantilla* (Miller).

bottom environment unfavourable to optimum coral growth and the presence of the Transcontinental Arch which acted as a barrier between the two areas.

Meagre data on the migration time of modern coral larvae suggests that most larvae become attached during the first 2 days of their existence, although some remain swimming for as long as 2 months (Connell 1973, p. 209). A pseudoplanktonic brephic-neanic growth habit would increase the time interval available for migration and thus provide a better explanation of the distribution pattern of *C. tantilla*. Species of *Cyathaxonia* have a long stratigraphical range and world-wide distribution despite their almost universal occurrence in dark, silty, argillaceous limestone and calcareous shale, lithofacies that reflect bottom conditions generally unfavourable to the growth of corals. The prevalence of this association prompted Hill (1938, pp. 5-9) to name the biofacies '*Cyathaxonia* Fauna'. A pseudoplanktonic growth habit in other species of *Cyathaxonia* might be a factor in the widespread distribution of the genus.

SYSTEMATIC PALAEONTOLOGY

Morphological terminology generally follows Hill (1935, 1956). The following abbreviations are used in the text: U.S. National Museum of Natural History, Washington, D.C., U.S.A. (USNM); U.S. Geological Survey, Washington, D.C., U.S.A. (USGS).

Family METRIOPHYLLIDAE Hill, 1939, emend. Rozkowska, 1969

Subfamily CYATHAXONIINAE Milne-Edwards and Haime, 1850

Genus CYATHAXONIA Michelin, 1847

1847 *Cyathaxonia* Michelin, p. 257.

1928 *Cyathocarinia* Soshkina, p. 376.

Type species. *Cyathaxonia cornu* Michelin, 1847, by subsequent designation of Milne-Edwards and Haime 1850. Lower Carboniferous (Tournaisian), Tournai, Belgium.

Diagnosis. Corallum small, ceratoid-cylindrical. Long, contratingent minor septa inserted alternately with metasepta according to metriophyllid septal plan. Columella tall, developed independently of major septa but in contact with them (pseudoseptal columella of Schouppé and Stacul 1961). Tabulae inclined downward towards epitheca. Dissepiments absent. Sides of septa may have rows of tubercles steeply inclined from the horizontal.

Discussion. Corals similar in most morphological aspects to the type species of *Cyathaxonia* have been found in strata ranging in age from Late Devonian (early Famennian) into Early Permian. Such morphologic similarity has resulted in recognition of the type species throughout the entire stratigraphic range of the genus, although subspecies and other species have been proposed for variations in the size and shape of the columella, septal number, size of the corallum, and length of the minor septa. Modifications of the septa have been variously called carinae, tubercles, or spines. Descriptions and illustrations of these modifications indicate that they consist of rows of rounded or pointed protuberances on the sides of the septa and not continuous ridges or flanges. Smith (1931, p. 8) pointed out that these are not true carinae.

Differences of opinion about the taxonomic significance of tuberculate v. non-tuberculate septa have resulted in different generic concepts. Carruthers (1913, p. 56) noted tubercles in the type species and in *C. rushiana* Vaughan from the Viséan, but did not find them in topotype specimens of the type species (Tournaisian) and did not consider the tubercles of diagnostic value. Schindewolf (1951, p. 99) found tuberculate septa in specimens of the type species from the Tournaisian of France and Viséan of Ireland but not in topotypes of *C. rushiana* (Viséan). He also noted all variations between forms having smooth septa and forms having well-developed tubercles and concluded that the presence or absence of tubercles has no taxonomic or chronologic significance. On the other hand, Soshkina (1928, p. 376) proposed the subgenus *Cyathocarinia* for Permian species of *Cyathaxonia* having tuberculate septa. Some subsequent authors (Soshkina *et al.* 1941, p. 41; Wang 1950, p. 205; Lecompte 1952, p. 482; Rozkowska 1969, p. 55) have continued to recognize *Cyathocarinia* as a subgenus of *Cyathaxonia*, whereas others (Soshkina 1939, p. 51; Kostic-Podgorska 1955, p. 170; Hill 1956, p. 264; Soshkina *et al.* 1962, p. 333; Ivanovskiy 1967, p. 23) regarded *Cyathocarinia* as a distinct genus.

Extensive published records of *Cyathaxonia* indicate that both tuberculate and nontuberculate forms are present throughout the long stratigraphic range of the genus. Much variation has been noted in the strength and abundance of the tubercles in forms that are very similar or identical in other respects. In the Mississippian species described herein from the United States, tubercles are not present in the higher parts of the calice or in the earlier parts of the corallum, making recognition difficult in many specimens without serial sectioning. Available data on North American Mississippian species suggest that the presence or absence of tubercles is one of the morphologic characters useful for discrimination of species. However, use of this character for generic or subgeneric discrimination does not result in taxonomic groups that are meaningful phylogenetically. Accordingly, I include both tuberculate and nontuberculate forms in *Cyathaxonia* and regard *Cyathocarinia* as a junior synonym.

Cyathaxonia tantilla (Miller)

Plate 12, figs. 1-18

- 1891 *Zaphrentis tantilla* Miller, p. 11, pl. 1, figs. 23, 24; Miller 1892, p. 621, pl. 1, figs. 23, 24; Keyes 1894, p. 111; [not] Girty 1903, p. 269.
- 1909 *Cyathaxonia tantilla* (Miller), Weller, p. 270; Grove 1935, p. 367, pl. 9, figs. 15-17; Easton 1944, p. 30, pl. 6, figs. 7, 8; pl. 16, figs. 16, 17; Conkin and Conkin 1954, p. 214, fig. 1A-D.
- 1960 *Cyathocarinia tantilla* (Miller), Sando, p. 168.
- 1909 *Cyathaxonia minor* Weller, p. 270, pl. 10, figs. 14-17; [?] Girty 1926, p. 24; [not] Davis 1956, p. 29, pl. 4, fig. 3.
- 1960 *Cyathaxonia arcuata* Weller?, Sando, p. 168, pl. 16, figs. 25-27.
- 1958 *Cyathaxonia cordillerensis* Easton, p. 13, pl. 1, figs. 14, 17, 18.

Distribution. Chouteau Limestone (Missouri), Fern Glen Limestone (Missouri, Illinois), Springville Shale (Illinois), Hannibal Shale (Illinois), Compton Limestone (Missouri), Sedalia Limestone (Missouri), St. Joe Limestone Member of Boone Formation (Missouri, Arkansas), Reeds Spring Limestone (Missouri), Shale below Rockford Limestone (Indiana), [?] limestone of Boone age (Texas), Paine Member of Lodgepole Limestone (Montana, Utah), Represo Formation (Sonora).

Diagnosis. *Cyathaxonia* having 28–36 (ordinarily 32) septa in ephebic stage. Corallum attaining a maximum length of about 20 mm and a maximum diameter of about 4.5 mm. Septa tuberculate in late neanic and ephebic stages.

Description of Utah and Montana specimens. Corallum ceratoid in brephic and neanic stages to cylindrical in ephebic stage (Pl. 12, figs. 3–5); cardinal side convex; commonly geniculate, vermiform, or planispirally coiled in brephic stage (Pl. 12, figs. 9–18); attaining a maximum length of 17 mm and a maximum diameter of 4.8 mm. Epitheca marked by strong longitudinal septal grooves and interseptal ridges, transverse rugae, and fine transverse striations (Pl. 12, figs. 3, 4, 9, 14) except in brephic stage, where only transverse striations are present (Pl. 12, figs. 12, 13). Calice as much as 6 mm deep at maturity. Septa number 32–36 at maturity (corallum diameter 4.5–4.8 mm).

Ephebic septal plan (Pl. 12, fig. 1) characteristic of the genus, consisting of cardinal septum in poorly defined fossula bounded by minor septa, major septa that reach columella but do not participate in its formation, counter septum on concave side of corallum, and minor septa that are contratingent on cardinal side of all major septa and fall slightly short of columella. Sides of septa usually have rows of tubercles that slope downward at an angle of 60°–80° from horizontal towards corallum axis (Pl. 12, fig. 8); tubercles present only in late neanic and ephebic stages (below floor of calice and immediately above floor of calice); septa ordinarily smooth in other parts of corallum but may have low ridges corresponding to rows of tubercles in calice. Columella smooth sided; ovate in cross-section with long diameter in cardinal-counter plane; 0.3–0.8 mm in short diameter and 0.9–1.5 mm in long diameter at base of mature calice; tapering to a blade-like point just below top of calice (Pl. 12, figs. 5, 8). Tabulae (Pl. 12, fig. 2) about 0.05 mm thick, concave upward, sloping upward from theca to columella; about five tabulae in vertical distance of 2 mm; not ordinarily seen in etched specimens.

Ontogeny. The earliest growth phase observed (Pl. 12, figs. 7, 16) is in the broken tip of several etched specimens (corallum diameter 0.4 mm), which have a single axial septum, to be differentiated later into cardinal and counter septa. In the next observed growth phase (Pl. 12, fig. 6), 6 protosepta (cardinal, counter, 2 alar, 2 counter lateral) are present at a corallum diameter of 0.7 mm. Development up to and including formation of the 6 protosepta is included in the brephic growth stage, which occupies the first 2 mm of corallum length to a corallum diameter of about 1 mm. The exterior of the corallum is without longitudinal ribbing in the brephic stage. The neanic stage is recognized for the part of the corallum that includes a complement of 7–31 septa to a corallum diameter of about 4 mm. During this stage, the corallum is characterized by maximum curvature and rapid expansion of its diameter. Formation of the columella as a discrete structure is initiated and continues into maturity. Rapid insertion of major and minor septa takes place according to the 'cyathaxoniid' septal plan described by Faurot (1909, pp. 75–80), Duerden (1906, p. 236, figs. 9–12), and Hill (1940, p. 194). In the ephebic stage, the corallum is essentially cylindrical and straight, showing very little expansion in diameter (to a maximum of 4.8 mm) and the insertion of few septa (maximum 32–36).

Discussion. North American species of *Cyathaxonia* have been differentiated mainly on the maximum size of the corallum, the maximum number of septa, the presence or absence of tubercles on the septa, and, to a lesser extent, on external ornamentation. Although statistical analysis of larger samples may ultimately prove otherwise, available evidence does not support separation of the Utah and Montana samples from samples of *C. tantilla* from the Mississippi Valley area. Easton (1944, p. 30) found only 28 septa at a corallum diameter of 3.5 mm in the 'most advanced stage observed' in the cotype lot, but Miller (1891, p. 12) recorded a septal number of

30 at a diameter larger than 3 mm in a cotype, Keyes (1894, p. 111) recorded a range of 20–32 septa in specimens from Missouri, and Conkin and Conkin (1954, p. 214) stated that the largest topotype specimens studied by them ‘constantly have 32 septa’ at corallum diameters of as much as 3.6 mm. The Utah and Montana specimens show a range of 30–36 septa at corallum diameters ranging from 3.5 to 4.8 mm in the largest coralla observed, but almost all the larger specimens have only 32 septa and a maximum diameter ranging from 3.5 to 4.5 mm (one specimen has 36 septa and one specimen has 34 septa).

C. minor Weller (1909, p. 270) is within the range of measurable characters of *C. tantilla*, as noted by Grove (1935, p. 368) and affirmed by Easton (1944, p. 30). *C. cordillerensis* Easton (1958, p. 13), characterized by 32–35 septa and a maximum corallum diameter of 4 mm, also cannot be separated from *C. tantilla*. Sando (1960, p. 168) incorrectly referred specimens of *C. tantilla* questionably to *C. arcuata* Weller. A summary of the distinguishing characteristics of the described North American species of *Cyathaxonia* (Table 3) indicates that *C. tantilla* differs from all others in having tuberculate septa. Most of the other species have a considerably larger corallum than *C. tantilla*, with the exception of *C. venusta*, distinguished by its cuneate corallum, and *C. winchelli*, a poorly known form that may be a synonym of *C. tantilla*.

Material studied. USNM 222513–222598. See list of localities for geographic locations and stratigraphic positions of collections.

TABLE 3. Summary of North American species of *Cyathaxonia*.

Species	Formation	Locality	Maximum septal number	Maximum length (mm)	Maximum diameter (mm)	Other distinguishing features
<i>C. tantilla</i> (Miller, 1891)	See text	See text	36	c. 20	c. 4.5	Tuberculate septa
<i>C. arcuata</i> Weller, 1909	Fern Glen Ls.	Missouri	36	36	7	
<i>C. winchelli</i> Rowley, 1900	Lower Burlington Ls.	„	36	16?	5?	
<i>C. cynodon</i> (Rafinesque and Clifford, 1820)	New Providence Sh.	Kentucky	36	25	7	Epithecal spines
<i>C. bordeni</i> Greene, 1900	„ „ „	Indiana	36	25	8	
<i>C. parva</i> Greene, 1900	„ „ „	„	50	30	10	
<i>C. venusta</i> Greene, 1904	Salem Ls.	„	34	15	5	Cuneate corallum
<i>C. ? iovaensis</i> Worthen, 1890	Ste. Genevieve Ls.	Iowa	c. 30	32	13	

LIST OF LOCALITIES

1. Brazer Canyon section, NW.¼SE.¼ Sec. 20, T. 11 N., R. 8 E., Rich County, Utah (see Sando *et al.* 1959, fig. 2 for geologic map). Paine Member of Lodgepole Limestone, lower 18.7 m. (USGS locs. 16801-PC–16832-PC) (see Table 1 for exact positions of individual samples).

2. Emma Canyon section, NE.¼SE.¼ Sec. 17, T. 11 N., R. 8 E., Rich County, Utah (see Sando *et al.* 1959, fig. 2 for geologic map). Paine Member of Lodgepole Limestone, 1.8–2.2 m above base (USGS loc. 16911-PC).

3. Sacajawea Peak section, south wall of cirque in NE.¼NW.¼ Sec. 27, T. 2 N., R. 6 E., Gallatin County, Montana. Paine Member of Lodgepole Limestone, 6.5 m above base (USGS loc. 20641-PC).

4. Logan section, SE.¼SW.¼ Sec. 25, T. 2 N., R. 2 E., Gallatin County, Montana (see Sando and Dutro 1974, pp. 4–8 for geologic map and section description). Paine Member of Lodgepole Limestone, lower 1.5 m (USGS loc. 17356-PC), 3 m above base (USGS loc. 17357-PC).

5. Baldy Mountain section, SE.¼NW.¼ Sec. 27, T. 7 S., R. 3 W., Madison County, Montana. Paine Member of Lodgepole Limestone, 0.8–1.4 m above base (USGS loc. 17911-PC), 6.2–7.7 m above base

(USGS loc. 17913-PC), 9.2–10.7 m above base (USGS loc. 17914-PC), 11.6–15.2 m above base (USGS loc. 17915-PC).

6. White Peak section, NE $\frac{1}{4}$ Sec. 2, T. 11 S., R. 4 E., Gallatin County, Montana (see Witkind 1969, pp. 89–93 for section description). Paine Member of Lodgepole Limestone, 6.3–17.1 m above base (USGS loc. 20164-PC).

7. Squaw Creek section, SE $\frac{1}{4}$ NE $\frac{1}{4}$ Sec. 34, T. 4 S., R. 4 E., Gallatin County, Montana. Paine Member of Lodgepole Limestone, 2.1–2.6 m above base (USGS loc. 20600-PC).

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COPROLITES CONTAINING PLANT MATERIAL FROM THE CARBONIFEROUS OF BRITAIN

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ABSTRACT. Coprolites containing plant material are described from the Middle Coal Measures (Westphalian B) of Swillington, near Leeds, West Yorkshire. Other possible coprolites from the Lower Carboniferous (Califerous Sandstone Series) of the Loch Humphrey Burn and Glenar buck localities in the Kilpatrick Hills, Strathclyde are also recorded. The Coal Measure specimens contain either lycopod megaspore fragments, indeterminate plant debris, or a large variety of microspores (attributable to Lycopsidea, Sphenopsida, Pteropsida; Filicinae, Gymnospermae, and Pteridospermae) whereas the Lower Carboniferous specimens consist mainly of rolled plant debris. It is suggested that these coprolites belonged to animal litter feeders and is direct evidence of animals eating vegetation in the Palaeozoic.

AFTER a recent symposium on animal/plant interrelationships in the Palaeozoic, Cox (1974) concluded that 'there seems little chance of a great variety of unequivocal evidence for the interaction between Palaeozoic plants and arthropods'. Although recent studies have shown that some interrelationships between animals and plants may have existed as early as the Devonian (Kevan *et al.* 1975), it remains true that very little direct evidence of animals feeding on plants has been brought forward.

Leaves of *Neuropteris* with holes, presumably made by an herbivorous animal, have been reported from Coal Measure sediments (Van Amerom 1966; Van Amerom and Boersma 1971) and similarly eaten leaves of *Glossopteris* have been described from the Karroo rocks of South Africa (Plumstead 1963). Borings, possibly made by insects, have been reported in *Trigonocarpus* seeds from the Carboniferous (Barnard, oral comm., see Cox 1974). Animal damage of plant axes (Kevan *et al.* 1975) and trigonotarbid arachnids within sporangia have been described from the Devonian Rhynie Chert (Rolfe in Kevan *et al.* 1975, pl. 56). Numerous examples of damaged stems have been reported from the Carboniferous (*Calamites*, Seward 1898, Stopes 1907; *Myeloxylon*, Holden 1910; lepidodendroid axis, Wilkinson 1930) but it is uncertain whether these wounds were caused by natural accidents or whether they were the result of animal damage. A few specimens of bored Carboniferous wood have been figured (i.e. *Sigillaria*, Geinitz 1855, pl. 8, fig. 1) and in one specimen borings have been shown to contain minute ($< 100 \mu\text{m}$) coprolites attributed to arthropods (Williamson 1880, pl. 20, figs. 65, 66). Other occurrences of damaged wood have been reviewed by Moodie (1923, pp. 99-108).

Unfortunately the morphology of Palaeozoic animals has not been of great help in the search for possible herbivores. The large Carboniferous 'centipede' *Arthropleura*, for example, was regarded as carnivorous on the basis of the nature of a supposed cephalic limb, but proved to have plant debris (?lycopod) in its gut (Rolfe and Ingham 1967).

The record of coprolites containing plant material has been very scanty. The contents of most coprolites are generally unidentifiable (phosphatized) or else they

contain animal remains and are generally attributed to fish (see occasional references in Häntzschel *et al.* 1968). Coprolites from coal balls have been figured by Mamay and Yochelson (1962) and those consist of partly macerated plant material, mostly epidermal (Mamay, pers. comm. 1976). Brief mention is made of coprolites containing plant material by Cox (1974) but no details are given.

Other coprolites containing spores and pollen have been reported from post-Palaeozoic rocks. Harris (1957) described, from the Jurassic of Yorkshire, small coprolites containing *Caytonia* pollen and leaf cuticle of both *Sagenopteris* and *Ginkgo*. Bryant and Williams-Dean (1975) described subfossil human coprolites which contained plant material and pollen which have given information on both early human diet and local vegetation.

The occurrence of coprolites containing plant remains from the Coal Measures of Yorkshire and the Calciferous Sandstone of the Kilpatrick Hills is further direct evidence that some animals were exploiting this food source in the Carboniferous. The predominance of plant material in the coprolites strongly suggests that they were produced by herbivores and are not the undigested waste products of plants accidentally eaten by carnivores.

DESCRIPTIONS

Coal Measures

Twelve small coprolites were found in residues obtained by disaggregating shales in hydrofluoric acid. The shales (flood plain deposits) were thin partings in poor coal one metre below and immediately above the Lodgett Coal, Swillington Brickworks, near Leeds, West Yorkshire (SE 384314, Godwin and Calver 1975). These residues also contained abundant megaspores, cuticles, and fusain including an early conifer (Scott 1974).

The coprolites are generally cylindrical in shape (up to 3×1 mm), although some have been flattened. They are of three main types: one containing mainly lycopod megaspore fragments, one containing a mixture of microspores, and one containing indeterminate plant debris. The megaspore fragments may be identified from the nature of their sculptural elements. One coprolite (Pl. 13, figs. 1, 2) contained only fragments of the sigillarian megaspore *Tuberculatisporites mammillarius* (Bartlett) (Pl. 13, figs. 7, 11) whereas another (Pl. 13, figs. 3, 9, 14) contained mainly fragments of lepidodendroid megaspores such as *Lagenicula subpilosa* (Ibrahim) (Pl. 13, figs. 8, 12). Occasional *Lycospora*, other unidentifiable microspores, and cuticle are also found.

Those coprolites containing microspores are more irregular in shape, often considerably flattened probably because of the greater compressibility of the more finely divided plant material. This type of coprolite has a wide range of composition, some containing an abundance of two types of spore (Table 1, specimens 10 and 12) and others a large number of types (Table 1, specimens 6 and 8, Pl. 13, figs. 5 and 6, Pl. 14, figs. 1–9). (Numerous sporangia are found in the same residues but are recognized by containing only a single species of spore, layering, and by the undamaged nature of the spores, Pl. 13, figs. 4, 10.) Many of the microspores are exceptionally well preserved although many are also broken. The spores which are

TABLE 1. The Composition of Coprolites from the Westphalian B of Yorkshire.
The specimens have been lodged in the Hunterian Museum, Glasgow (FSC 2061-2072).

Specimen no.	1	2	3	4	5	6	7	8	9	10	11	12
LYCOPSIDA—MEGASPORES												
<i>Tuberculatisporites mammillarius</i> (Bartlett)	A											
<i>Lagenicula subpilosa</i> (Ibrahim)							C					
Indeterminate			C				A	R				
LYCOPSIDA—MICROSPORES												
<i>Lycospora</i> (Schopf, Wilson and Bentall)		R				O	O	R				A
<i>Densosporites</i> (Berry)								O				C
cf. <i>Crassispora</i> (Bharadwaj)	R							?R				
? <i>Cristatisporites</i> (Potonié and Kremp)			O			O						
SPHENOPSIDA—MICROSPORES												
<i>Calamospora</i> Schopf, Wilson and Bentall						?A		?O				
? <i>Laevigatisporites</i> Ibrahim										A		
PTEROPSIDA—MICROSPORES												
FILICINAE												
cf. <i>Cyclogranisporites</i> Potonié and Kremp								?R				
<i>Raistrickia</i> (Schopf, Wilson and Bentall)								O				
cf. <i>Verrucosisporites</i> (Ibrahim)			A									
cf. <i>Savitrissporites</i> Bharadwaj								R				
GYMNOSPERMAE												
? <i>Florinites</i> Schopf, Wilson and Bentall				A								
PTERIDOSPERMAE												
<i>Schopfipollenites</i> Potonié and Kremp								R				
UNKNOWN AFFINITY												
cf. <i>Ahrensisporites</i> Potonié and Kremp								C				
cf. <i>Pustulatisporites</i> Potonié and Kremp						C		?C				
Indeterminate					O	O		C				
OTHER PLANT MATERIAL												
Indeterminate cuticle				?A	O	R	O	O	?A			
Indeterminate wood			C			O						
Indeterminate plant material	A	C			A	O	O	O	A	R	A	

R = Rare, O = Occasional, C = Common, A = Abundant.

recorded represent both a wide variety of morphologies and a number of diverse plant groups including lycopods (*Lycospora* and *Densosporites*, Pl. 13, fig. 5), ferns (*Raistrickia*, Pl. 14, fig. 8), pteridosperms (*Schopfipollenites*, Pl. 14, fig. 7), and sphenopsids (*Calamospora*) (Potonié 1962, 1965; Potonié and Kremp 1954).

It is concluded that these pellets are genuine coprolites, and not burrow fills, peat pellets, or sporangia, because of the repetition of constant shape and the heterogeneity of plant material. From the variety of plant material in the coprolites it appears that the animals concerned were more likely to have been litter feeders rather than direct cone or leaf feeders. There is no conclusive evidence that these coprolites all belong to the same type of animal, but from the general size and shape this seems a strong possibility.

There are a number of different kinds of animal, mainly arthropod, which may have been eating the plant litter and produced these coprolites. Although cuticle of

arachnid type (Pl. 14, fig. 14, L. J. Wills and I. Strachan, pers. comm. 1975) has been found in this deposit there is no evidence to suggest that this was the animal responsible.

Lower Carboniferous, Calciferous Sandstone Series

(i) Loch Humphrey Burn

This material, from the Walton Collection in the Hunterian Museum, Glasgow (prefix Pb to numbers) comes from the Loch Humphrey Burn plant bed (Smith 1964) and is preserved as compression fossils. These 'coprolites' (Pl. 14, fig. 13) are fairly common and range in length from 20 to 26 mm (e.g. Pb 3313, 3314a, b, 2507, 2516) and when found unsquashed are approximately 7 mm in diameter (Pl. 14, fig. 12, Pb 3314c). The flattened cylinders generally show four longitudinal ridges as seen on a cleaved bedding surface (Pl. 14, fig. 13). In cross-section they show twelve prominent ridges (Pl. 14, fig. 12). It is not fully understood how in the same bed most of these 'coprolites' are flattened whilst one remains unsquashed. There is no way to prove that the two types of fossils are related, short of cleaving open the unsquashed specimen to look at the longitudinal view, but from the nature of the shape, a cylinder with prominent ridges, it would seem likely that they are similar objects. It will need, therefore, further specimens before the nature of preservation is fully understood.

When macerated these cylinders yield unidentifiable plant debris. They are thought not to be either burrow fills or peat pellets because of their constant shape, but there remains the possibility that they may be some poorly preserved plant organ rather than a coprolite, although the latter is favoured. There are no data concerning the animals that might have produced these ?coprolites.

EXPLANATION OF PLATE 13

Westphalian B coprolites and associated plant fragments from shaly partings below and above the Lidgett Coal, Swillington, West Yorkshire. All pictures were taken with a Cambridge S600 Scanning Electron Microscope (S.E.M.), the specimens having been coated with gold in a Polaron Sputter-Coating Unit E5000.

Figs. 1-3, 9, 14. Coprolites containing megaspore fragments. 1, whole coprolite, Table 1, specimen 1, $\times 40$ (FSC 2061). 2, fragment of megaspore *Tuberculisporites mammillarius* (Bartlett) from the same specimen, $\times 150$ (FSC 2061). 3, whole coprolite, Table 1, specimen 7, $\times 40$ (FSC 2067). 9, detail of megaspore fragment of *Lagenicula subpilosa* (Ibrahim) from the same specimen, $\times 250$ (FSC 2067). 14, megaspore fragments, microspores, and plant debris from the same specimen, $\times 250$ (FSC 2067). Figs. 4, 10. Dispersed sporangium from the same horizon. 4, detail of spores, *Calamospora* Schopf, Wilson and Bentall, $\times 160$ (FSC 2073). 10, whole sporangium, $\times 15$ (FSC 2073). Figs. 5, 6, 13. Coprolites containing microspores and plant debris. 5, whole coprolite, Table 1, specimen 3, $\times 15$ (FSC 2063). 6, detail of same specimen with ?*Cristatisporites* (Potonié and Kremp), $\times 600$ (FSC 2063). 13, detail of coprolite, Table 1, specimen 9, with abundant plant debris, $\times 225$ (FSC 2069). Figs. 7, 8, 11, 12. Megaspores from the same horizon. 11, *Tuberculisporites mammillarius*, $\times 20$ (FSC 2076). 7, detail of distal face, $\times 150$ (FSC 2074). 12, *Lagenicula subpilosa*, $\times 25$ (FSC 2075). 8, detail of spines, $\times 275$ (FSC 2075).

All specimens have been lodged in the Geology Collection of the Hunterian Museum, Glasgow.



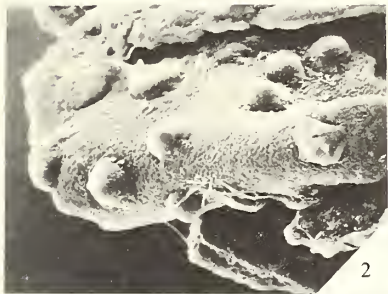
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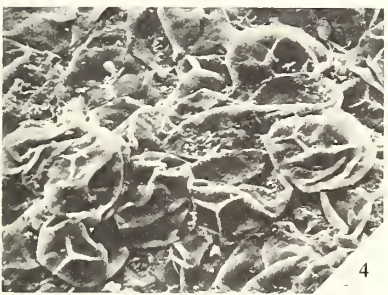
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SCOTT, plant debris in Carboniferous coprolites

(ii) Glenarbuck

Three slides, in the Walton Collection, Hunterian Museum, Glasgow (FSC 779–781), show cross-sections of what have been interpreted (on Walton's slide label) as coprolites. These have a circular, although slightly irregular cross-section (Pl. 14, fig. 10) with a diameter of 5 mm (FSC 781 has a diameter of 1 mm but this may be because only the tapered end of the coprolite was sectioned). The three slides are probably peels from the same specimen. The plant material inside the ?coprolite is layered (Pl. 14, fig. 11) consisting mainly of stelar and woody elements and other unidentifiable plant material. For these specimens, however, there is less evidence that these are coprolites; they may be simply pellets of petrified peat.

No animal remains have been found in association with these ?coprolites.

DISCUSSION

Which animals produced these coprolites and which Palaeozoic animals were herbivores is a matter of speculation. Numerous types of insects were present in the Coal Measures, some of which may have been herbivores (phytophagous). It has been suggested that other arthropod groups such as the Collembola and Arachnida may have been litter feeders, as they are today (Tillyard 1931). The Collembola are also thought to have been spore feeders (Smart and Hughes 1973) as have some of the trigonotarbid arachnids already cited. Kevan *et al.* (1975) note that spores are often one of the alternative food sources 'adopted' by carnivorous (zoophagous) arthropods if animal food is lacking.

Of the insects, especially ground-dwelling species, cockroaches (Dictyoptera) were present in the Carboniferous (Müller 1963). I have examined the faecal pellets from an extant genus of the phytophagous cockroach, *Blaberus*, which is 6–7 cm

EXPLANATION OF PLATE 14

Figs. 1–9. Westphalian B coprolites from shaly partings below and above the Lidgett Coal, Swillington, West Yorkshire. (S.E.M. as Pl. 13.) These specimens (including fig. 14) have been lodged in the Geology Collection of the Hunterian Museum, Glasgow. 1, whole coprolite, Table 1, specimen 6, $\times 25$ (FSC 2066). 2, detail of same specimen with a triangular microspore with conate ornament, ?*Pustulatisporites* Potonié and Kremp, $\times 600$ (FSC 2066). 4, whole coprolite, Table 1, specimen 8, $\times 15$ (FSC 2068). 3, detail of the same specimen with ?*Cyclogranisporites* Potonié and Kremp, $\times 450$ (FSC 2068). 5, detail of the same specimen with *Lycospora* (Schopf, Wilson and Bentall) and ?*Denosporites* (Berry), $\times 600$ (FSC 2068). 6, detail of the same specimen with numerous microspores including ?*Savitrissporites* Bharadwaj and ?*Ahrensissporites* Potonié and Kremp, $\times 300$ (FSC 2068). 7, detail of the same specimen with *Schopfipollenites* Potonié and Kremp, $\times 250$ (FSC 2068). 8, detail of the same specimen with *Raistrickia* (Schopf, Wilson and Bentall), $\times 600$ (FSC 2068). 9, detail of the same specimen with microspores including ?*Ahrensissporites* Potonié and Kremp, $\times 500$ (FSC 2068).

Specimens shown in figs. 10–13 are from the Walton Collection in the Hunterian Museum, Glasgow.

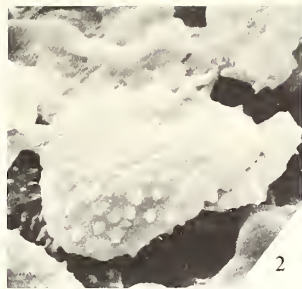
Figs. 10, 11. Cross-sections of ?coprolites from the Calciferous Sandstone Series of Glenarbuck. 10, whole cross-section, $\times 4$ (FSC 780). 11, detail showing plant debris and stelar fragments, $\times 30$ (FSC 780).

Figs. 12, 13. ?Coprolites from the Calciferous Sandstone Series, Loch Humphrey Burn. 12, cross-section, $\times 4$ (Pb 3314c). 13, longitudinal cleavage compression, $\times 2$ (Pb 2576).

Fig. 14. Animal cuticle (?Arachnid) from the shales below the Lidgett Coal, Swillington, West Yorkshire, $\times 8$ (A 2618).



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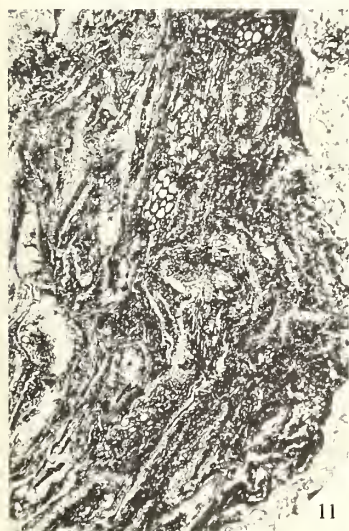
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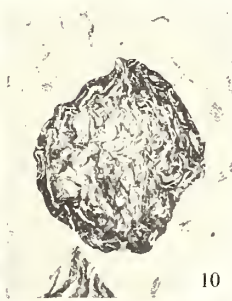
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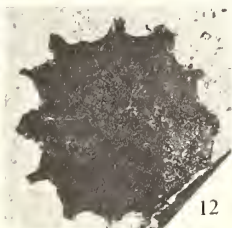
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SCOTT, plant debris in Carboniferous caprolites

long. These are small, 3 mm $\times$ 1 mm, roughly cylindrical, and occasionally show longitudinal striations. Smaller species would presumably produce smaller faecal pellets (perhaps comparable in size and shape to the Coal Measure specimens). Smart and Hughes (1973) suggest that the 'probosces of Palaeodictyoptera and Megasectoptera could have been used as a probe to work over cones and capsules of the plants of that time (Carboniferous) for spores and pollen and perhaps especially for megaspores . . .' which Kevan *et al.* (1975) observe must have represented a particularly nutritious food source for insects. The eating of spores by arthropods, it has been suggested, is likely to have contributed to spore dispersal and even when the spores have passed through the animals' gut some of them may still have remained viable (Chaloner 1976).

Other arthropods which are thought to have been phytophagous include the myriapods (Kevan *et al.* 1975; Rolfe and Ingham 1967). These include the millepedes which have Palaeozoic representatives (Hoffman 1969) and have been shown in some figures to be eating plant material including *Lepidodendron* (Hoffman 1969). I have examined the faecal pellets of an extant African millepede, 9 cm long. These consist of plant debris and measure 6 mm $\times$ 3 mm. The size of the faecal pellets, however, is not directly related to the length of the animal but to a combination of body weight and the quantity of food eaten at any one time (Edwards 1974). *Arthropleura*, a member of an extant group of myriapods, has been shown to be phytophagous. A juvenile specimen with lycopod fragments in its gut (Rolfe and Ingham 1967) might have produced faecal pellets about 4 mm in diameter (measured from Pl. 13, fig. 8). The adult animal which grew to 1.5 m long must have produced larger faecal pellets, perhaps the size of the Lower Carboniferous specimens, although the genus *Arthropleura* is only known from Upper Carboniferous deposits (Rolfe 1969).

Although most groups of extant arachnids are zoophagous some mites (Acarida) are phytophagous (Wallwork 1967). Most, however, are very small (less than 1 mm, Harding and Stuttard 1974). Some Palaeozoic forms are found up to 8 mm in length (Petrunkévitch 1955) and may have produced faecal pellets in the order of 1 mm long.

Few early vertebrates are thought to have been herbivores although the Upper Palaeozoic amphibian *Scincosaurus* which has spatulate teeth may be such an animal (A. Girvan, pers. comm.).

CONCLUSIONS

Considering the quantity of plant material available for exploitation as a food source, in the Carboniferous, it is surprising that previously very little direct evidence of herbivores has been found as ultimately all land fauna is dependent on land vegetation, forming the basis of an extensive food chain.

The occurrence of coprolites containing spores and plant tissue is direct evidence that at least some animals were exploiting this food source in the Carboniferous.

Acknowledgements. I would like to thank Mr. D. W. Brett for bringing the Lower Carboniferous material to my attention, G. Armitage and Sons for permission to visit their Swillington Quarry, Dr. W. D. I. Rolfe for the loan of specimens in his care, and Dr. P. Banham and Professor W. G. Chaloner for their helpful comments. This work was carried out during the tenure of an N.E.R.C. Studentship which is gratefully acknowledged.

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CLASSIFICATION OF THE TRILOBITE *PSEUDAGNOSTUS*

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ABSTRACT. Eighty-eight species assigned or assignable to *Pseudagnostus sensu lato* are divided into two broad divisions based on the position of the glabellar node with respect to the anterior or anterolateral glabellar furrows and anterolateral lobes. A spectaculate division, in which the node lies to the rear of the anterior furrow and to the rear of the anterolateral lobes, is divided into nine species groups which are recognized by degree of effacement of external morphology, shield shape, border morphology, glabellar morphology, pygidial spinosity, and metamerism. Three spectaculate species groups, *bulgosus*, *communis*, and *cyclopyge*, are referred to *Pseudagnostus* Jaekel, 1909, *sensu stricto*; one, *contracta*, to *Pseudagnostina* Palmer, 1962; and one, *securiger*, to *Sulcatagnostus* Kobayashi, 1937, these latter taxa being regarded as subgenera of *Pseudagnostus*. Four other spectaculate species groups, *araneavelatus*, *bilobus*, *canadensis*, and *clavus*, are classified with *Neoagnostus* Kobayashi, 1955, pending clarification of the taxonomic status and concepts of *Euplethagnostus* Lermontova, 1940, and *Pseudorhaptagnostus* Lermontova, 1940. *Hyperagnostus* Kobayashi, 1955 and *Machairagnostus* Harrington and Leanza, 1957 are synonymized with *Neoagnostus*. A papilionate division, in which the axial glabellar node lies between the anterolateral lobes and interrupts the course of the anterior furrow, consists of two species groups, *convergens* and *clarki*, which are assigned to *Rhaptagnostus* Whitehouse, 1936. The generic name *Plethagnostus* Clark, 1923 is suppressed.

THE genus *Pseudagnostus* was erected by Jaekel in 1909 for species of *Agnostus* possessing a short pygidial axis and an 'endolobe', currently termed a deuterolobe (see Öpik 1963, p. 31).

Jaekel (1909, p. 400) designated as type species *Agnostus cyclopyge* Tullberg (1880, p. 26; pl. 2, fig. 15a, c, cephalon and pygidium respectively), which occurs in the *Olenus* Zone and the zone of *Parabolina spinulosa* with *Orusia lenticularis*, at Andrarum, Skåne, and other localities in Sweden (Tullberg 1880, p. 26; Westergård 1922, p. 117; 1944, pp. 32–33; 1947, p. 22).

The type specimens, reported by Tullberg (1880, p. 26) to have been deposited in the Geological Museum, University of Lund, have not been identified. According to Dr. Jan Bergström (pers. comm. 1973), the specimens were numbered but there is no evidence that they were deposited in the type collections. Although they may not be lost, it might be difficult to differentiate them from other material in the collections from Andrarum. Until the specimens are positively located, the concept of *Pseudagnostus cyclopyge* is based on specimens collected from the type locality, figured by Westergård (1922, pl. 1, fig. 7, cephalon, Lund University Lo 3066t, and 8, pygidium, Lo 3067t), and reproduced here on Plate 15, figs. 1–2. Westergård's specimens were obtained from beds containing *O. lenticularis*.

Recent research (Öpik 1967; Shergold 1972, 1975) classifies the genus *Pseudagnostus* with *Pseudagnostinae* Whitehouse, 1936, which is regarded as a subfamily of *Diplagnostidae* Whitehouse, 1936, as emended by Öpik (1967).

When it was erected, a mere handful of species could be assigned to *Pseudagnostus*; but by now it is possible to assign no fewer than eighty-eight species, listed in Appendix B. They are united by the possession of a deuterolobe similar to that seen in the type species. Excluding this characteristic, a wide range of forms has

been included in *Pseudagnostus*, with the result that any original concept of the genus has become substantially changed, and it has become necessary to discuss the genus in a *sensu lato* manner. This proliferation of species is directly responsible for the present review, as *Pseudagnostus sensu lato* is common in the late Cambrian of northern Australia, currently under investigation by the author. There, a range of pseudagnostinid forms spans a wide interval of late Cambrian time, and is potentially useful for the close zonation of upper Cambrian strata (Shergold 1975).

AGE AND DISTRIBUTION OF *SENSU LATO* TAXON

The time span of *Pseudagnostus sensu lato* is long: it first appears in the earliest late Cambrian (early Mindyallan *Erediaspis eretes* Zone in Australia; early Tuorian *Agnostus pisiformis*/*Homagnostus fecundus* Zone in Siberia; and early Dresbachian *Cedaria* Zone in North America) and continues into the earliest Ordovician (Canadian, *Symphysurina* and *Kainella* faunas in North America). Pseudagnostoid species are particularly common in correlatives of the late Mindyallan *Glyptagnostus stolidotus* Zone in Australia, in the late Dresbachian *Aphelaspis* and *Dunderbergia* Zones in North America, in the early Franconian and early Shidertan *Elvinia* and *Irvingella* Zones in North America and Siberia respectively, and in the late Shidertan *Lotagnostus trisectus*/*Peltura* Zone in Siberia and its equivalent post-Idamean/pre-Payntonian interval in Australia.

The genus is cosmopolitan, having lived in seas peripheral to Precambrian crustal masses now forming the nuclei of Europe, Eurasia, eastern Asia, North America, South America, Australia, and Antarctica. Within these seas, *Pseudagnostus* appears to have favoured habitats within ocean-facing environments (Palmer 1972), at the ocean-neritic boundary (Robison 1972) which approximates the boundary between carbonate belt and outer detrital belt as interpreted by Palmer (1960a, 1969, 1972, 1973) and Robison (1960a). Its species are commonly found in the deep subtidal

EXPLANATION OF PLATE 15

- Figs. 1-2. *Pseudagnostus* (*Pseudagnostus*) *cyclopyge* (Tullberg, 1880). 1, LULo 3066, topotype cephalon (Westergård 1922, pl. 1, fig. 7), $\times 7$. 2, LULo 3067, topotype pygidium (Westergård 1922, pl. 1, fig. 8), $\times 7$; the concept of *Pseudagnostus* currently rests on these specimens.
- Figs. 3-4. *Pseudagnostus* (*Pseudagnostus*) *ampullatus* Öpik, 1967. 3, CPC 5899, paratype cephalon, $\times 11.5$. 4, CPC 5896, holotype pygidium, $\times 11$; an *en grande tenue* species preserved in limestone.
- Figs. 5-6. *Pseudagnostus* (*Pseudagnostus*) *bulgosus* Öpik, 1967. 5, CPC 5904, paratype cephalon, $\times 12.5$. 6, CPC 5901, holotype pygidium, $\times 12$.
- Figs. 7-8. *Pseudagnostus* (*Pseudagnostus*) *communis* (Hall and Whitfield, 1877). 7, USNM 24557e, silicone replica of hypotype cephalon (Palmer 1955, pl. 19, fig. 20), $\times 8.5$. 8, USNM 24557d, replica of hypotype pygidium (Palmer 1955, pl. 19, fig. 21), $\times 12$.
- Figs. 9-10. *Pseudagnostus* (*Pseudagnostus*) *josepha* (Hall, 1863). 9, 10, silicone replicas of cotypes, AMNH 311, preserved as sandstone moulds, $\times 8$; illustrated for comparative purposes.
- Figs. 11-12. *Pseudagnostus* (*Pseudagnostina*) *contracta* (Palmer, 1962). 11, USNM 143149b, replica of paratype cephalon, $\times 16$. 12, USNM 143150, replica of holotype pygidium, $\times 16$.
- Fig. 13. *Pseudagnostus* (*Sulcatagnostus*) *securiger* (Lake, 1906). GSM 57650, replica of holotype, $\times 6$.
- Figs. 14-15. *Rhaptagnostus clarki* (Kobayashi, 1935). 14, USNM 146887, paratype cephalon, $\times 9.5$. 15, USNM 93062, holotype pygidium, $\times 9.5$.



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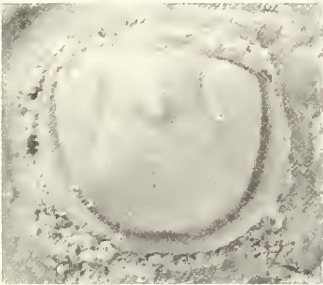
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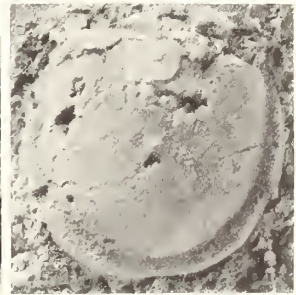
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(Laporte 1971, for terminology) outer detrital belt dark shale, silt, and finely laminated limestone deposited on the oceanic margins of carbonate banks, in deep subtidal interbank channels, and other places with current connection to the open ocean. In such environments pseudagnosti presumably contribute to late Cambrian equivalents of Agnostid Community Assemblages 1 and 2 of Jago (1973). Species of *Pseudagnostus* are also found in coarse calcarenite and debris layers, allochthonously deposited on beaches or in channels. Pseudagnosti are less commonly found in the sandstones and dolomites of the inner detrital belt (Palmer's (1960a, 1969, 1973) terminology). When found in inner detrital depositional environments they appear to retain a more or less constant morphology for an appreciable length of time, e.g. *P. josepha* (Hall), and are not repeatedly replaced in the biostratigraphical section by rapidly evolving taxa to the same extent as they appear to be in outer detrital and carbonate belt environments. Maximum species diversification is thus observed at the oceanic/neritic boundary, where warm shelf currents and cooler oceanic currents mingle.

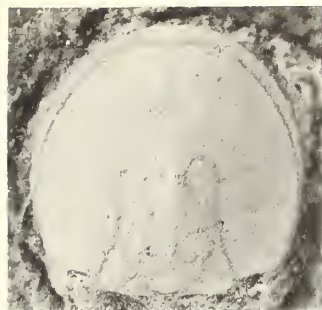
MORPHOLOGY

In assessing morphology it is necessary to know if specimens are testiferous or moulds, as well as the nature of the matrix. Little information, other than the shapes of the cephalic and pygidial shields and a vague lobation and perhaps furrowing, can be gained from sandstone moulds, as is evident from the cotypes of *P. josepha* (Hall 1863) (Pl. 15, figs. 9–10). By way of contrast, the species illustrated in Plate 15, figs. 3–4 and Plate 16, figs. 3–6 demonstrate the range of morphological features shown by both exoskeletons and moulds preserved in limestone.

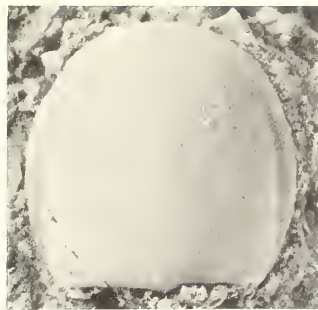
The distinction between morphology exhibited by moulds and by tests is basic to understanding both the reasons for the proliferation of species assigned to *Pseudagnostus*, and the difficulties in subdividing them at generic and subgeneric levels.

EXPLANATION OF PLATE 16

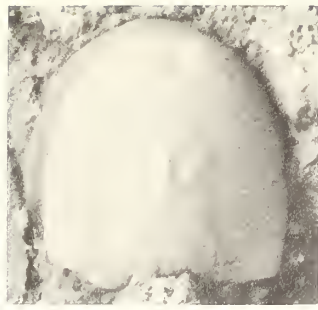
- Figs. 1–2. *Rhaptagnostus convergens* (Palmer, 1955). 1, USNM 123563, paratype cephalon, $\times 10$. 2, USNM 123562, holotype pygidium, $\times 9.5$.
 Figs. 3–6. *Rhaptagnostus bifax* (Shergold, 1975). 3, CPC 11596, holotype cephalon preserved with exoskeleton, $\times 10$. 4, CPC 11656, paratype pygidial exoskeleton, $\times 10$. 5, CPC 11597, replica of parietal surface of paratype cephalon, $\times 10$. 6, CPC 11667, parietal surface of paratype pygidium, $\times 7$.
 Figs. 7–8. *Neoagnostus bilobus* (Shaw, 1951). 7, USNM 124467, replica of paratype cephalon, $\times 16$. 8, USNM 124468, replica of holotype pygidium, $\times 12.5$.
 Figs. 9–10. *Neoagnostus canadensis* (Billings, 1860). 9, GSC 858, replica of paratype cephalon, $\times 10$. 10, GSC 858b, replica of lectotype pygidium, $\times 9$.
 Figs. 11–12. *Neoagnostus araneavelatus* (Shaw, 1951). 11, USNM 124467, replica of paratype cephalon, $\times 20$. 12, USNM 124466, replica of holotype pygidium, $\times 22$.
 Figs. 13–15. *Neoagnostus clavus* (Shergold, 1972). 13, 14, CPC 8454, paratype cephalon, lateral and dorsal views respectively, $\times 9$. 15, CPC 8451, paratype pygidium, $\times 10.5$.
 Fig. 16. *Neoagnostus aspidoides* Kobayashi, 1955. Replica of holotype cephalon, GSC 12745, $\times 7$.
 Fig. 17. *Neoagnostus* [*Hyperagnostus*] *binodosus* (Kobayashi, 1955). Replica of holotype cephalon, GSC 12747, $\times 7$.
 Fig. 18. *Neoagnostus* [*Trinodus*] *priscus* (Kobayashi, 1955). Replica of holotype pygidium, GSC 12751, $\times 7.5$.



1



3



5



2



4



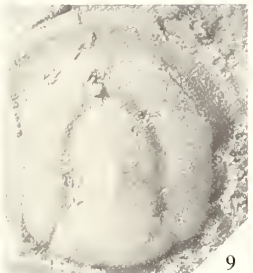
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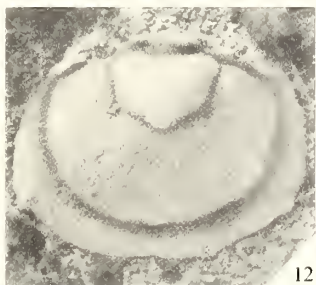
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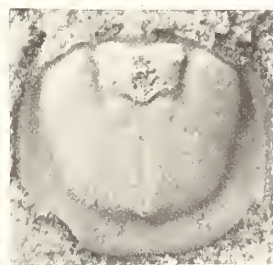
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18



15

Some species have been described from moulds alone, others from exoskeletons, both generally in an uncritical manner. Reference to Plate 15, figs. 3–4 will show that supposedly diagnostic differences may readily be found if preservation is ignored. When such differences become the basis for generic taxa, obvious problems arise.

In an earlier paper (Shergold 1975), and here, a major distinction is made between the morphology of the outer surface of the exoskeleton, and that of its internal surface. The latter can be observed directly on the inner surface of silicified or phosphatized exoskeletons; most commonly, however, it is interpreted from impressions on the surface of its internal mould. Such surfaces are here termed 'parietal surfaces', and their morphology, which is a negative of the inner surface of the exoskeleton, is termed 'parietal morphology'.

From the classificatory point of view, the morphology of the outer surface of the exoskeleton gives information on lobes and furrows, and the positions of nodes and spines. Parietal morphology, on the other hand, gives basic anatomical information relating to the internal musculature, and the vascular and caecal systems of the organism, as deduced from the occurrence and distribution of various scrobiculations, muscle scar impressions, and pits.

Morphological terminology applicable to Pseudagnostinae (*inter alia*) has been defined exhaustively elsewhere (Öpik 1963, 1967; Shergold 1972, 1975). Terminology used in the classification presented here, and not readily evident from these papers or requiring further comment, is summarized in Appendix A.

LOCATION OF MATERIAL

Observations on personally collected Australian specimens have been supplemented by the acquisition of replicas of the types of most established taxa, and the study of museum materials in Europe, North America, and Japan.

Located material is in the collections of repositories abbreviated as follows:

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	British Museum (Natural History), London, U.K.
BYU	Brigham Young University, Provo, Utah, U.S.A.
CPC	Commonwealth Palaeontological Collection, Canberra, A.C.T., Australia.
GMAN	Geological Museum, Kazakhstan Academy of Science, Alma Ata, U.S.S.R.
GSC	Geological Survey of Canada, Ottawa, Canada.
GSCh	Geological Survey of China, Peking, China.
GSM	Institute of Geological Sciences, London, U.K.
HAN	Cambrian Catalogue, Geological Survey, Hanover, Germany.
IGAL	Institute of Arctic Geology, Leningrad, U.S.S.R.
IGGN	Siberian Research Institute for Geology, Geophysics, and Mineral Raw Materials (SNIIGGIMS), Novosibirsk, U.S.S.R.
IGUT	Institute of Geology, University of Tokyo, Japan.
IPP	Institute of Palaeontology, Peking, China.
LU	Laval University, Quebec, Canada.
LULo	Lund University, Lund, Sweden.
MCZ	Museum of Comparative Zoology, University of Harvard, Cambridge, Massachusetts, U.S.A.
MNHU	Museum für Naturkunde, Humboldt University, East Berlin, D.D.R.
MSM	Manchurian Science Museum, Mukden, Manchuria, China.

NHMM	Natural History Museum, Mendoza, Argentina.
NUP	National University, Peking, China.
NZAR	Athropod Register, New Zealand. Geological Survey, Lower Hutt, New Zealand.
OGM	Oklahoma Geological Survey, Tulsa, Oklahoma, U.S.A.
OUM	Oxford University Museum, Oxford, U.K.
RMS	Riksmuseet, Stockholm, Sweden.
SGU	Geological Survey of Sweden, Stockholm, Sweden.
THU	Tsing-hua University, Peking, China.
UBA	University of Buenos Aires, Argentina.
UQ	University of Queensland, St. Lucia, Queensland, Australia.
USGS	United States Geological Survey, Washington, D.C., U.S.A.
USNM	National Museum of Natural History (formerly United States National Museum), Washington, D.C., U.S.A.
UT	University of Texas, Austin, Texas, U.S.A.
YPM	Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.
ZSGU	Museum of the West Siberian Geological Board, Novokuznetsk, U.S.S.R.

CLASSIFICATION

For the purposes of this review species assigned to the following closely related or synonymous genera and subgenera were considered: *Pseudagnostus* Jaekel, 1909; *Plethagnostus* Clark, 1923; *Rhaptagnostus* Whitehouse, 1936; *Sulcatagnostus* Kobayashi, 1937a; *Pseudorhaptagnostus* Lermontova, 1940; *Euplethagnostus* Lermontova, 1940; *Neoagnostus* Kobayashi, 1955; *Hyperagnostus* Kobayashi, 1955; *Machairagnostus* Harrington and Leanza, 1957; and *Pseudagnostina* Palmer, 1962. These species, together with others previously classified elsewhere, are listed in Appendix B. Three other pseudagnostinid genera were examined but are not considered further in the classification: *Litagnostus* Rasetti, 1944, because of the extreme difficulty in assessing this very effaced form; *Xestagnostus* Öpik, 1967, because of its uncharacteristically simple articulating device and different pygidial diverticular structure; and *Oxyagnostus* Öpik, 1967, because of its distinct deuterolobe morphology which cannot be confused with that of *Pseudagnostus* (see Öpik 1967, pp. 159–161).

For the purposes of classification the most obvious differences between species are carapace shape and degree of effacement. Less obvious, but seemingly more important from the anatomical point of view, is the position of the axial glabellar node with respect to the anterior furrow and anterolateral glabellar furrows. Species fall broadly into two divisions. Spectaculate pseudagnosti are those in which the glabellar node lies to the rear of the anterolateral lobes. Two groups are discernible: those in which the anterior furrow is transverse, straight, or gently curved backwards and the anterolateral lobes are distinctly separated sagittally, e.g. *Pseudagnostus communis* (Hall and Whitfield), as refigured by Palmer (1955) (see Pl. 15, figs. 7–8); and those in which the anterior furrow is V-form, and the anterolateral lobes meet, and may fuse, sagittally, e.g. *Neoagnostus bilobus* (Shaw, 1951) (Pl. 16, fig. 7). Papilionate pseudagnosti are those in which the node interrupts the course of the anterior furrow, dividing it into V-form anterolateral furrows, and lies between the anterolateral lobes as, for example, in *Rhaptagnostus clarki* (Kobayashi, 1935a) (Pl. 15, fig. 14).

An intermediate condition, in which the node interrupts the course of the anterior furrow, dividing it into V-form anterolateral furrows, but still lies slightly behind the anterolateral lobes, is included within the spectaculate division of this classification, but could possibly be regarded as a distinct category. The condition appears to be gradational, but the observed differences could be interpreted as the result of preservation.

The spectaculate condition embraces the bulk of species assigned to *Pseudagnostus sensu lato*. Spectaculate pseudagnosti occur earlier, being first found in the earliest late Cambrian of Australia, North America, and Siberia, and disappear later, in the early Ordovician of North America. The intermediate forms occupy a relatively narrow time interval during the late Cambrian, in the *Elvinia* and *Conaspis* Zones and their correlatives in Europe, Siberia, and Australia. Papilionate pseudagnosti arise during this time interval, at least in Australia (Shergold, in prep.), and continue into the earliest Ordovician (in Mexico). Thus there appears to be a time-related forward migration of the axial glabellar node.

The function of the axial glabellar node is not known: nor is the reason for its apparent migration. Some speculation may, however, be offered. Parietal surfaces of some pseudagnostinid cephalons show the axial and terminal glabellar nodes connected by an axial carina which itself bears a longitudinal sulcus (Shergold 1975, pl. 3, fig. 5; text-fig. 15), structures which can be interpreted as having supported the gut and a dorsal tubular heart. The high spot of the axial glabellar node is frequently perforated, particularly in limestone moulds. Ruedemann (1916) interpreted the glabellar node of *Cryptolithus* as a dorsal median eye containing a single fluid lens, and such lenses may have occupied the perforated regions of both cephalic and pygidial axial nodes in agnostids, their function being to assess the intensity and direction of light and orient the animal within the water column. Harris and Mason (1956) have shown that experimentally blinded *Daphnia* are 'more sensitive to light than normal ones and show a greater capacity for adaptation to light during the cycle of vertical migration' (p. 285). Thus the lack of a compound eye, also lacking in agnostids, is no bar to photokinesis. Harris and Mason (1956) have suggested for *Daphnia* an interrelationship of the photosensitive system, the nervous system, and reflex control of the heart rate. The cephalic and pygidial nodes of pseudagnosti may well, therefore, be connected with photosensitive systems in direct connection with the blood vascular system, the combination facilitating orientation and migration of the animal in the water column.

Öpik (1961a, p. 417) has considered that the agnostid stomach consists of anterior and posterior sacs connected by a constricted passage beneath the anterior transverse glabellar furrow. In pseudagnosti, however, the lateral portions of this furrow merely represent the internally raised anterior margins defining the anterolateral muscle attachment areas which, depending on the length of muscle, would not necessarily constrict the stomach. Any interruption or modification of the course of the anterior furrow, as is apparent, is therefore more likely to reflect a modification of the muscle attachment areas. The positioning of the axial glabellar node between the anterolateral muscle attachment areas in papilionate pseudagnosti may have resulted in the lateral separation of the bases of the appendages attached there, and/or restricted the area of attachment of such appendages, which would presum-

ably be restricted in size. This situation may be contrasted with that seen in the spectaculate species here assigned to *Neoagnostus*, in which the attachment areas may meet axially. The anterolateral muscle scars are generally the largest of the pseudagnostinid cephalon, and are thought to represent the areas of attachment for mandibular appendages. Thus modification of the shape and position of the mandibular attachment areas could reflect difference in feeding habit. Hence this classification is based on anatomical features fundamental to the animal.

While the position of the axial node and its relationship to the anterolateral muscle scars is regarded here as basic in the classification of Pseudagnostinae, other factors are of considerable value in recognizing species groups. Some can be recognized by degree of effacement, whereas in others this characteristic varies presumably in response to environmental conditions. Ideally species groups should comprise taxa in which the condition of effacement is relatively constant, and in practice this is difficult to attain owing to the differing preservation exhibited by established species. Ideally genera should embrace effaced, partially effaced, and *en grande tenue* species groups.

Degree of effacement influences observation on the condition of other characteristics used in this classification. Although all pseudagnosti are deuterolobate, as deduced from parietal morphology, the degree of tumidity of the deuterolobe and degree of incision of its associated bounding accessory furrows vary considerably. Externally effaced and partially effaced pseudagnosti are generally weakly deuterolobate and non-plethoid parietally. Species externally *en grande tenue* are usually strongly deuterolobate and plethoid, but there are exceptions, e.g. the *bilobus* species group described below. In similar manner degree of deliquiation (Shergold 1975) is related to effacement. Externally effaced and partially effaced species are non-deliquiate or subdeliquiate: their moulds are likely to have subdeliquiate and deliquiate marginal furrows. *En grande tenue* species are deliquiate, and their moulds strongly so: generally cephalae are more strongly deliquiate than their assigned pygidia.

Carapace shape, which may be subcircular, subovoid, subquadrate, or subrectangular, is relatively constant in some, but not all, species groups. Pygidial segmentation, which can be assessed from the number of muscle scars and apodemes on the internal surface of the test, or the number of muscle-scar impressions and notulae on the parietal surface, may be related to shield shape. As a generalization, elongated pygidia have more paired muscle attachment areas, and by inference segments, than subquadrate ones. Similarly, the position of the posterolateral pygidial spines may be related to the shield shape: elongate pygidia have anteriorly situated spines with respect to the termination of the deuterolobe, whereas subquadrate pygidia have retrally sited spines. Shield shapes, and consequently spine positions, may change during morphogenesis. Most species in which meraspid pygidia have been observed have a subquadrate shield with retrally positioned spines. Change in shape occurs with the development of the deuterolobe during late meraspid morphogenesis (see Palmer 1955, pp. 94–96, pl. 20 for *P. communis*).

Morphological features associated with the anterior portion of the pygidial axis have not been fully exploited in this classification. While the clarity of the transverse furrows, and the axial furrows bounding the pre-deuterolobe axis is dependent on

the degree of effacement shown by the exoskeleton in general, the degree of anterior divergence of the axial furrows varies considerably, even within species. Among some species assigned here to *Neoagnostus*, a third pair of muscle scars is consistently enclosed by axial furrows. In others, their visibility is dependent on degree of effacement, cf. *N. bilobus* (Shaw) (Pl. 16, fig. 8) and *N. araneavelatus* (Shaw) (Pl. 16, fig. 12), and manner of preservation (exoskeleton or mould). A third pair of muscle-scar impressions is often also visible on exfoliated specimens of *Pseudagnostus* and *Rhaptagnostus*, but in these is never bounded by axial furrows (e.g. Pl. 16, fig. 2). The characteristic is variable, but may have some use in differentiating isolated pygidia of *Neoagnostus* from those of *Pseudagnostus* or *Rhaptagnostus*.

The position of the pygidial axial node is quite variable, but unlike the axial glabellar node this variation is inconsistent. It lies across the sagittal length of the second axial segment, is apparently connected to the axial region between the muscle scars of the first segment, and extends rearwards between the scars of the third segment to varying extents. In *Pseudagnostus* and its subgenera, it terminates generally at the front of the third intermuscle scar area (Pl. 15, figs. 2, 4, 6, 10, 13); in *Rhaptagnostus* it may extend considerably further between the third pair of muscle scars (Pl. 16, figs. 2, 6); but in *Neoagnostus* its extent is only consistent within individual species (cf. Pl. 16, figs. 8, 10, 12, 15). Size, shape, and transverse separation of the muscle scars evidently influence observation of the extent of this feature.

In many pseudagnosti the axial pygidial node is bilobed, having anterior and posterior high spots (see Pl. 15, figs. 4, 6; Pl. 16, figs. 2, 6), and is bifid, being posteriorly cleft (Pl. 16, fig. 6). On some specimens the anterior high spot is perforated, like the axial glabellar node. The axial pygidial node is therefore a complicated structure which presumably had multiple functions.

DELINEATION OF SPECIES GROUPS

Species are grouped here on the combinations of characteristics listed above. Considerable variation occurs in some of the groups whereas others are quite homogeneous. The groups are not species, although synonymous species may exist within them. Species groups may constitute subgenera, but apart from those lying at the limits of variation, e.g. possessing three pygidial spines (*securiger* group) or are extremely effaced (*contracta*), for which names are already available (*Sulcatagnostus* and *Pseudagnostina* respectively), it is preferred not to name them formally at this time. Not all species have yet been examined at first hand, particularly Russian taxa, and some may further modify the concepts presented herein.

Of the species listed those marked with an asterisk signify that type or subsequently figured material has been examined in museum collections, or from silicone replicas.

A. SPECTACULATE PSEUDAGNOSTI

Araneavelatus group (Pl. 16, figs. 11–12)

Nominal species. **Pseudagnostus araneavelatus* Shaw, 1951, pl. 24, p. 113, figs. 12–16, holotype pygidium USNM 124466, paratype USNM 124467, remainder untraced, early Ordovician, *Missisquoi* Zone, Vermont, U.S.A.

Diagnosis. Cephalon subcircular, *en grande tenue* or partially effaced, non-deliquate or subdeliquate, spectaculate, tendency to develop prominent furrows to the rear of the anterolateral lobes, anterolateral furrows generally externally effaced, median preglabellar furrow absent. Pygidium subcircular, partially effaced, non-deliquate, non-plethoid, weakly deuterolobate, spines posteriorly situated close to a transverse line drawn across the rear of the deuterolobe, possibly eight late holaspid metameres.

Other species

**Pseudagnostus coronatus* Shergold, 1975, pp. 85–87, pl. 6, figs. 1–6, holotype cephalon CPC 11692, paratypes CPC 11693–11697.

Pseudagnostus cyclopygeformis (Sun) *sensu* Kobayashi 1960, p. 341, pl. XIX, fig. 6, IGUT no number, non fig. 7 (*clarki* group), IGUT no number.

**Phalacronia cyclostigma* Raymond, 1924, p. 397, pl. 12, fig. 4, holotype pygidium YPM 4747.

**Pseudagnostus denticulatus* Shergold, 1975, pp. 87–89, pl. 8, figs. 1–5, holotype cephalon CPC 11705, paratypes CPC 11706–11709.

**Pseudagnostus* sp. *C* Shergold, 1975, pp. 91–92, pl. 7, figs. 5–7, CPC 11714–11716.

Age and distribution. Late Cambrian: pre-Payntonian/post-Idamean, *Rhaptagnostus clarki patulus* with *Caznaia squamosa* through *R. bifax* with *Neoagnostus denticulatus* Assemblage-Zones (Shergold 1975), western Queensland, Australia; late Changshanian; *Kaolishania* Zone, Tanggok, South Korea.

Early Ordovician; *Missisquoia* Zone, Vermont, U.S.A.

Comments. The Australian species listed here as constituting the *araneavelatus* group were previously placed in the *clavus* group (Shergold 1975). They are nevertheless distinguishable from the *clavus* and *bilobus* groups (below) by their rounded shield shapes and proportions. The arrangement of glabellar lobes and furrows shown is common to all groups.

Bilobus group (Shergold 1975, p. 92) (Pl. 16, figs. 7–8)

Nominal species. **Pseudagnostus bilobus* Shaw, 1951, pp. 112–113, pl. 24, figs. 17–22, holotype pygidium USNM 124468, paratypes USNM 124469–124471, early Ordovician, *Missisquoia* Zone, Vermont, U.S.A.

Diagnosis. Cephalon subquadrate, generally *en grande tenue*, deliquate or subdeliquate, spectaculate, tendency to over-deepen furrows both in front and behind the anterolateral glabellar lobes; a median preglabellar furrow is generally present. Pygidium subcircular or subquadrate, partially effaced, deliquate or subdeliquate, non-plethoid, weakly deuterolobate, spines generally sited on a transverse line across the rear of the deuterolobe or behind it; a third pair of muscle-scar impressions is incorporated into the axis behind and adjacent to the pygidial axial node.

Other species

**Neoagnostus aspidoides* Kobayashi, 1955, pp. 473–474, pl. VII, fig. 5, holotype cephalon GSC 12745, non fig. 4, geragnostoid pygidium GSC 12746, pl. IX, fig. 5 (line-drawing).

**Hyperagnostus binodosus* Kobayashi, 1955, p. 475, pl. VII, fig. 2, holotype cephalon GSC 12747, non fig. 3, geragnostoid pygidium GSC 12748, pl. IX, fig. 4 (line-drawing).

Aagnostus cyclopyge Tullberg *sensu* Sun 1939, p. 30, pl. 1, figs. 1–3, repository and numbers not known.

**Pseudagnostus longicollis* Kobayashi, 1966, p. 283, fig. 7, IGUT no number.

**Trinodus priscus* Kobayashi, 1955, p. 476, pl. VII, fig. 6, holotype pygidium GSC 12751.

**Pseudagnostus quasibilobus* Shergold, 1975, pp. 94–95, pl. 12, figs. 1–7, holotype cephalon CPC 11717, paratypes CPC 11718–11723.

Machairagnostus tmetus Harrington and Leanza, 1957, p. 64, figs. 6–7, holotype (complete specimen) UBA 1297, paratypes UBA 1195, 1292–1294, 1298.

*Undetermined pseudagnostid, Robison and Pantoja-Alor 1968, p. 780, pl. 97, fig. 23, USNM 158886.

Age and distribution. Late Cambrian: Payntonian, *Neoagnostus quasibilobus* with *Tsinania nomas* Assemblage-Zone (Shergold 1975), western Queensland, Australia; Fengshanian, Yunnan; Wanwanian, Jehol Block, China.

Early Ordovician: Oaxaca Province, Mexico; *Missisquoia* Zone, Vermont, U.S.A.; Tremadocian, *Parabolina argentina* Zone, Argentina; *Missisquoia*, *Symphysurina*, and *Kainella-Evansaspis* faunas, British Columbia, Newfoundland, Canada.

Comments. Like the *clavus* group from which it is possibly derived, the *bilobus* group represents an assemblage of species linked through the orientation of their glabellar furrows. Cephalons are, in general, preserved *en grande tenue*, whereas pygidia have depressed deuterolobes and effaced accessory furrows. The retrol position of the pygidial spines is constant among the species cited.

Bulgosus group (Pl. 15, figs. 5–6)

Nominal species. **Pseudagnostus bulgosus* Öpik, 1967, pp. 156–158, pl. 38, fig. 8; pl. 62, figs. 1–4, Mindyallan zones of *Erediaspis eretes* and *Glyptagnostus stolidotus*, western Queensland, Australia. Designated holotype pygidium CPC 5901, paratypes CPC 5902–5904, 5656.

Diagnosis. Cephalon subovoid, *en grande tenue*, spectaculate, deliquiate, anteriorly converging acrolobe, median preglabellar furrow absent. Pygidium subovoid, *en grande tenue*, convergent flanks, subdeliquiate, plethoid, deuterolobate, restricted pleural lobes, very small spines in advance of a transverse line drawn across the rear of the deuterolobe in holaspides.

Other species

**Oedorhachis boltonensis* Resser, 1938, p. 50, pl. 10, figs. 19–20, cotypes USNM 94869.

Pseudagnostus levatus E. Romanenko in Romanenko and Romanenko, 1967, pp. 75–76, pl. 1, figs. 18–19, holotype pygidium ZSGU 133/135, paratype ZSGU 133/136.

**Oedorhachis mesleri* Resser, 1938, p. 50, pl. 10, figs. 13–14, cotypes USNM 94864.

**Pseudagnostus nganasanicus* Rosova, 1964, pp. 27–28, pl. 16, figs. 3–4, holotype pygidium IGGN 113/875, paratype IGGN 113/928.

Possibly also included in the *bulgosus* group is:

Pseudagnostus mestus Öpik, 1967, pp. 155–156, pl. 62, figs. 5–6, holotype pygidium CPC 5906, paratype cephalon CPC 5905.

Age and distribution. Late Cambrian: Mindyallan, *Erediaspis eretes* and *Glyptagnostus stolidotus* Zones, western Queensland, Australia; Dresbachian, *Cedaria* Zone, Virginia and Tennessee, U.S.A.; Tuorian, zones of *Aagnostus pisiformis* with *Homagnostus fecundus* and *Glyptagnostus stolidotus*, Kulyumbe River, Katun River, and Lena River, Siberian Platform, U.S.S.R.

Comments. This is the earliest species group referable to *Pseudagnostus sensu lato*, homogeneous in content and character.

Canadensis group (Pl. 16, figs. 9–10)

Nominal species. *Aagnostus canadensis* Billings, 1860, p. 304, fig. 3a–b, lectotype pygidium (designated Rasetti (1944) GSC 858b, paratype cephalon GSC 858, refigured as *Pseudagnostus canadensis* (Billings), (Rasetti 1944, p. 234, pl. 36, figs. 8–13, GSC 858, 858b, LU 1104a–d), late Cambrian, Lévis Conglomerate, Quebec, Canada.

Diagnosis. Cephalon subquadrate, *en grande tenue*, wide borders with deliquiate marginal furrows, spectaculate, anterolateral glabellar furrows effaced, but those to

rear of anterolateral lobes prominent, median preglabellar furrow present parietally. Pygidium subquadrate, *en grande tenue*, wide borders with deliquiate marginal furrows, strongly deuterolobate, strongly plethoid, restricted pleural areas, retral spines.

Other species. Rasetti (1944) has synonymized *Agnostus janei* Clark, 1923, p. 124, fig. 8; 1924, p. 19, fig. 5, MCZ 1696.

Age and distribution. Late Cambrian: Lévis Conglomerate, Quebec, Cow Head Group conglomerates, Newfoundland (C. H. Kindle, pers. comm.).

Comments. The *canadensis* group is readily recognized by its strongly *en grande tenue* condition and fused anterior and anterolateral glabellar lobes. Most probably it has been derived from the same ancestral stock as the *araneavelatus* group.

Clavus group (Shergold 1975, p. 82) (Pl. 16, figs. 13–15)

Nominal species. **Pseudagnostus clavus* Shergold, 1972, pp. 31–34, pl. 3, figs. 1–8, holotype pygidium CPC 8453, paratypes CPC 8451, 8454–8456; also Shergold, 1975, pp. 84–85, pl. 8, figs. 6–12, CPC 11689–11704, late Cambrian, *Rhaptagnostus bifax* with *Neoagnostus denticulatus* and *R. clarki maximus* with *R. papilio* Assemblage-Zones (Shergold 1975), western Queensland, Australia.

Diagnosis. Cephalon subquadrate, *en grande tenue* or partially effaced, wide borders with subdeliquiate or deliquiate marginal furrows, spectaculate, prominent V-form anterolateral glabellar furrows, weakly chevronate furrows to rear of anterolateral lobes, rhomboid anterior lobe, median preglabellar furrow absent, proximally present, or present. Pygidium subquadrate to subovoid, *en grande tenue* or partially effaced, non-deliquiate or subdeliquiate, non-plethoid or subplethoid, generally weakly deuterolobate, retral pygidial spines, seven to eight metameres in late holaspides.

Other species

**Rhaptagnostus acutifrons* Troedsson, 1937, pp. 22–24, pl. 1, fig. 9, RMS number not known.

**Pseudagnostus cavernosus* Rosova, 1960, pp. 12–14, pl. 1, figs. 1–4, holotype pygidium IGGN 76/557, paratype 74/556; holotype refigured Rosova in Khalfin 1960, p. 165, pl. Cm-XVIII, fig. 4.

Pseudorhaptagnostus punctatus Lermontova, 1940, p. 126, pl. 49, fig. 14, 14a, repository and numbers not known.

Pseudorhaptagnostus simplex Lermontova, 1951, pp. 12–13, pl. 2, figs. 11–15, non figs. 16–17, designated holotype is pygidium fig. 11, repository and numbers not known; also *Pseudagnostus simplex* (Lerm.) in Nikitin 1956, pl. XIV, fig. 5, non fig. 4.

Euplethagnostus subangulatus Lermontova, 1940, p. 126, pl. 49, fig. 15, 15a, repository and numbers not known.

**Pseudagnostus vulgaris* Rosova, 1960, pp. 14–16, pl. 1, figs. 5–13, holotype pygidium IGGN 76/645, paratypes IGGN 74/524, 75/582, 76/578, 76/647, 76/653, 76/654, 76/656, 79/633; refigured Rosova in Khalfin 1960, p. 165, pl. Cm-XVIII, fig. 5a–c.

**Pseudagnostus* sp. *A* Shergold, 1975, pp. 89–90, pl. 7, figs. 1–2, CPC 11710–11711.

**Pseudagnostus* sp. *B* Shergold, 1975, pp. 90–91, pl. 7, figs. 3–4, CPC 11712–11713.

Questionably belonging to this group are:

**Homagnostus* cf. *acutus* Kobayashi, 1938, pp. 173–174, pl. XV, fig. 4, cephalon GSC 11979.

Pseudagnostus bituberculatus Ivshin in Khalfin, 1960, p. 165, pl. Cm-XVIII, fig. 6a–b, repository and numbers not known.

Pseudagnostus quadratus Lazarenko, 1966, pp. 46–47, pl. 1, figs. 24–29, holotype cephalon IGAL 36/8907, paratype numbers not known.

Age and distribution. Late Cambrian: post-Idamean/pre-Payntonian, *Rhaptagnostus clarki patulus* with *Caznaia squamosa* through *R. c. maximus* with *R. papilio* Assemblage-Zones (Shergold 1975), western Queensland, Australia; Shidertan, zones of *Irvingella* to *Lotagnostus trisectus/Peltura* (Ivshin and Pokrovskaya 1968), Kazakhstan, Sayan Altai, Olenek River, U.S.S.R.; early Franconian, *Elvinia* Zone, British Columbia, Canada; Changshanian, *Kaolishania* Zone, South Korea; late Cambrian, Tianshan, China.

Comments. As presently constituted, this is a heterogeneous group that varies considerably in degree of effacement and deliquiation, and somewhat in shield shape. Species are presently linked in possessing a V-form anterior glabellar furrow, rhomboidal anterior lobe, and seven or eight pygidial metameres. Many Russian species are, however, inadequately known and may be wrongly classified within this group. Possibility exists for further dividing the group on presence or absence of a median preglabellar furrow. As far as is known only Australian representatives lack a well-defined median preglabellar furrow externally.

Communis group (Palmer 1968, p. 30) (Pl. 15, figs. 7–8)

Nominal species. **Aagnostus communis* Hall and Whitfield, 1877, pp. 228–229, pl. 1, figs. 28–29, late Cambrian, Dunderberg Shale, locality unknown, Nevada, *sensu* Palmer (1955, pp. 94–96, pl. 19, figs. 20–21, USNM 24557).

Regardless of synonymy, many specimens have been referred to *Pseudagnostus communis* (Hall and Whitfield), viz:

*Palmer, 1954, pp. 720–721, pl. 76, figs. 1–3, UT 32205, USNM 123309, UT 32169.

*Palmer, 1960b, p. 61, pl. 4, figs. 3–4, USNM 136832a–b.

*Robison, 1960b, p. 14, pl. 1, figs. 2, 5, BYU 10911–0–975a–b.

*Rasetti, 1961, p. 109, pl. 23, figs. 13–17, USNM 143054–143055.

Bell and Ellinwood, 1962, p. 389, pl. 51, figs. 7–21, UT 34842–34856.

*Lochman, 1964, p. 47, pl. 9, figs. 32–36, USNM 140664a–e.

*Rasetti, 1965, p. 39, pl. 10, figs. 23–25, USNM 144547.

*Palmer, 1968, pp. 29–30, pl. 7, figs. 5, 10, USNM 136832a–b.

Diagnosis. Cephalon subcircular to subovoid, partially effaced, narrow borders with non-deliquiate or subdeliquiate marginal furrows, spectaculate, anterior glabellar furrow usually transverse rectilinear, median preglabellar furrow invariably present. Pygidium subcircular to subovoid, partially effaced, subplethoid, weakly to strongly deuterolobate, narrow borders with subdeliquiate marginal furrows, spines well in advance of a transverse line drawn across the rear of the deuterolobe, eight late holaspide metameres.

Other species

**Aagnostus coloradoensis* Shumard, 1861, p. 218, cephalon USNM 26928.

**Pseudagnostus convergens* Palmer *sensu* Lochman and Hu 1959, p. 412, pl. 57, figs. 1–6, USNM 137088a–f.

**Aagnostus josepha* Hall, 1863, p. 178, pl. 6, figs. 54–55; 1867, p. 169, pl. 1, figs. 54–55; refigured in Shimer and Shrock, 1944, pl. 251, figs. 5–6, cotypes AMNH 311.

**Pseudagnostus josephus* (Hall) [*sic*] *sensu* Grant 1965, p. 108, pl. 13, figs. 13–14, USNM 142409–142410.

**Pseudagnostus* cf. *P. laevis* Palmer *sensu* Grant 1965, p. 108, pl. 14, figs. 34–35, USNM 142319.

**Pseudagnostus latus* Kobayashi, 1938, p. 171, pl. XVI, figs. 23–24, cotypes GSC 11989–11990, ?non figs. 40–41, GSC 11991–11992.

**Aagnostus neon* Hall and Whitfield, 1877, pp. 229–230, pl. 1, figs. 26–27, cotypes USNM 24568; refigured Palmer 1955, pp. 94, 96, pl. 19, figs. 16, 19, and synonymized with *communis*.

**Pseudagnostus orientalis* Kobayashi, 1933, pp. 98–99, pl. IX, figs. 20–22, IGUT unnumbered [holotype fig. 22]; 1935b, pp. 110–111, pl. III, figs. 7–11, 23, IGUT unnumbered.

**Agnostus prolongus* Hall and Whitfield, 1877, pp. 230–231, pl. 1, figs. 30–31, cotypes USNM 24637; refigured Palmer, 1955, pp. 98–99, pl. 19, figs. 17, 22.

**Pseudagnostus prolongus* (Hall and Whitfield) *sensu* Lochman and Hu, 1959, pp. 412–413, pl. 57, figs. 7–16, USNM 137089a–k.

**Pseudagnostus* cf. *prolongus* (Whitfield) [*sic*] *sensu* Lochman and Hu, 1960, p. 812, pl. 95, fig. 36, USNM 138218.

Pseudagnostus rotundatus Lermontova, 1940, p. 125, pl. 49, fig. 12, 12a–c, repository and numbers not known.

Pseudagnostus rotundatus Lermontova *sensu* Pokrovskaya in Tchernysheva *et al.* 1960, p. 464, pl. 2, fig. 7, repository, numbers, and location (apart from Siberia) unknown.

**Pseudagnostus sentosus* Grant, 1965, pp. 108–109, pl. 9, figs. 2–3, 5, holotype pygidium USNM 142284, paratypes USNM 142283, 142434.

**Pseudagnostus vulgaris* Rosova *sensu* Palmer, 1968, p. 30, pl. 12, fig. 5, USNM 146845, ?non fig. 6, USNM 146661.

**Pseudagnostus* spp., Palmer, 1962, p. 21, pl. 2, figs. 16, 21, 26, USNM 143147a–b, 143148.

**Pseudagnostus* sp., Robison and Palmer, 1968, pp. 169–170, photo 3, USNM 158031.

Questionably included in the *communis* group are also:

**Pseudagnostus gyps* (Clark) *sensu* Rasetti, 1959, p. 381, pl. 51, figs. 13–14, USNM 136929.

Pseudagnostus cyclopygeformis (Sun) (*pars*) *sensu* Endo in Endo and Resser, 1937, p. 316, pl. 65, figs. 19–22, non pl. 68, figs. 8–16, MSM 1080, 1157, 1249, 1260, 2582 (unplaced).

Age and distribution. Late Cambrian: late Dresbachian zones of *Aphelaspis*, *Dicantropyge*, and *Dunderbergia*; Franconian zones of *Elvinia*, *Conaspis* (*Taenicephalus*), *Ptychaspis* (*Idahoia*), and *Saukia* (*Illaenurus*), Nevada, Utah, Texas, Idaho, Montana, Wyoming, Alabama, Wisconsin, Minnesota, Maryland, Tennessee, Alaska, U.S.A.; *Elvinia* Zone, British Columbia, Canada; late Tuorian, zone of *Glyptagnostus reticulatus*; Shidertan, zone of *Plicatolina perlata*, Yakutia, Olenek River, U.S.S.R. (Lazarenko 1966; Ivshin and Pokrovskaya 1968); Paishanian, *Chuangia* Zone, Liaotung and Taitzuho, Manchuria, and South Korea.

Comments. A *Pseudagnostus communis* species group initially was recognized by Palmer (1968, p. 30), although no unifying or diagnostic characteristics were listed. The assignment of species made here differs from those listed by Palmer.

As constituted here, the *communis* group exhibits variation in shield shape and to some extent the position of the axial glabellar node. Species intermediate between spectaculate and papilionate exist, e.g. *P. communis sensu* Rasetti, 1961, *P. neon* (Hall and Whitfield), and the specimens ascribed to *P. prolongus* by Lochman and Hu (1959), which appear to link the *communis* group morphologically to that of *Rhaptagnostus clarki* (following). Within a single paradigm there is a more or less constant degree of effacement.

Contracta group (Pl. 15, figs. 11–12)

Nominal species. **Pseudagnostina contracta* Palmer, 1962, p. F21, pl. 2, figs. 18–20, 22–25, holotype pygidium USNM 143150, paratypes USNM 143149a–b, 143151–143152, 143153a–b, late Cambrian, Dresbachian, *Cedaria* Zone, Nevada, Alabama, U.S.A.

Diagnosis. Cephalon subovoid to subquadrate, effaced or partially effaced, deliquiate and subdeliquiate marginal furrows, strongly spectaculate, rectilinear transverse anterior furrow, median preglabellar furrow absent. Pygidium subovoid to subquadrate, effaced or partially effaced, subdeliquiate marginal furrows, non-plethoid, weakly deuterolobate, spines variable but usually posteriorly positioned close to the rear of the deuterolobe.

Other species

**Pseudagnostina vicaria* Öpik, 1967, pp. 158–159, pl. 55, fig. 4; pl. 63, figs. 8–9, holotype pygidium CPC 5918, paratypes CPC 5816, 5919.

**Pseudagnostina?* sp. indet. (aff. *vicaria* sp. nov.) Öpik, 1967, p. 159, pl. 63, fig. 10, CPC 5920.

Öpik (1967, p. 150) has noted that species described as *Agnostus douvillei* Bergeron by Walcott (1913, p. 100, pl. VII, fig. 3, 3a–b; pl. XI, figs. 6–7) and Resser and Endo (*in* Endo and Resser 1937, p. 162, pl. 49, figs. 25–28) may belong to *Pseudagnostina*. *A. koerferi* Monke (1903, pp. 111–114, pl. 3, figs. 1–9; pl. 9; Woodward 1905, pp. 211–215, 251–255, pl. 13, fig. 5), synonymized with *douvillei* by Walcott (1913, p. 100), thus may also belong to *Pseudagnostina*. Wolfart (1974, p. 90) has synonymized other references to *A. douvillei* (Mansuy 1916; Kobayashi 1935b; Lu 1957; Lu *et al.* 1965), with his *Pseudagnostus kobayashii*, which is tentatively included here in the *cyclopyge* group. The type cephalon of *A. douvillei* Bergeron (1899, p. 503, pl. XIII, fig. 3, repository and number unknown), cannot be readily interpreted. The species *Oedorhachis boltonensis* Resser, which Palmer (1962, p. 21) regarded as belonging to *Pseudagnostina*, is here placed in the *bulgosus* species group.

Age and distribution. Late Cambrian: Mindyallan, *Glyptagnostus stolidotus* Zone, western Queensland, Australia; Dresbachian, *Cedaria* Zone, Alabama, Nevada, U.S.A.; Kushanian, *Drepamura–Stephanocare* interval, Vietnam, China (Shantung), Manchuria (Liaotung), South Korea.

Comments. This group may represent an effaced derivation from the *bulgosus* group.

Cyclopyge group (Pl. 15, figs. 1–2)

Nominal species. **Agnostus cyclopyge* Tullberg, 1880, p. 26, pl. II, fig. 15a, c, as interpreted by Westergård 1922, pp. 116–117, pl. 1, figs. 7–8 (LULo 3066t–3067t), late Cambrian, zones of *Olenus* and *Parabolina spinulosa* with *Orusia lenticularis*, Andrarum, Skåne, Sweden (see discussion in introduction to this paper). Of other specimens which have been assigned to this species, the following have been traced:

**Agnostus cyclopyge* Tullberg *sensu* Lake 1906, pp. 27–28, pl. II, figs. 21–22, OUM number not known and BMNH 58494 respectively; also **Pseudagnostus cyclopyge* (Tullberg) *sensu* Rushton *in* Taylor and Rushton 1971, p. 26, pl. VIII, figs. 1–2, GSM Ru1202, 1042.

Diagnosis. Cephalon subovoid to rounded subquadrate, *en grande tenue*, wide borders with strongly deliquiate marginal furrows, spectaculate, subovoid to sub-circular acrolobe, transverse rectilinear anterior furrow in early representatives becoming curved backwards or V-form in later ones, median preglabellar furrow present. Pygidium subovoid to rounded subquadrate, *en grande tenue*, wide borders with strongly deliquiate marginal furrows, plethoid, deuterolobate, spines generally well forwards of a transverse line across the rear of the deuterolobe.

Other species

**Pseudagnostus anpullatus* Öpik, 1967, p. 150, pl. 61, figs. 7–11, holotype pygidium CPC 5896, paratypes CPC 5897–5900.

Pseudagnostus angustilobus Ivshin, 1956, pp. 19–21, pl. 9, figs. 11–15, 18–23, holotype cephalon GMAN 69/926, paratypes GMAN 73/926, 68/926, 72/926, 78/926, 79/926, 85/926, 84/926, 83/926, 123/926, 84/926.

Agnostus chinensis Dames, 1883, pp. 27–28, pl. 2, figs. 18–19; Kobayashi 1937b, p. 434, pl. 17, fig. 14a–b, material destroyed; Schrank 1974, pp. 622–623, pl. 1, figs. 1–7, MNHU K302, T893.2, 893.3, 894.1, 895.1; *non Agnostus chinensis sensu* Walcott, 1913, pp. 99–100, pl. 7, figs. 4–5; *non Pseudagnostus chinensis* (Dames) *sensu* Lu *et al.* 1965, p. 41, pl. 4, figs. 3–5 = *Peronopsis rakuroensis* (Kobayashi) *fide* Kobayashi (1937b, p. 434).

Pseudagnostus communis (Hall and Whitfield) *sensu* Lu *et al.* 1965, pp. 41–42, pl. 4, figs. 6–8, repository and numbers not known.

Homagnostus convexus Chu, 1959, pp. 88–89, pl. 1, figs. 3–4, *non* figs. 1–2, 5–7, also *in* Lu *et al.* 1965, p. 20, pl. 1, fig. 10, *non* figs. 8–9, IPP 9411–9412.

- **Pseudagnostus* cf. *cyclopyge* (Tullberg) sensu Whitehouse, 1936, p. 100, pl. X, fig. 8, UQ F3188; probably equivalent to *Pseudagnostus* cf. *vastulus* Whitehouse sensu Öpik, 1963, pp. 50–53, text-fig. 13, CPC 4302.
- **Pseudagnostus idalis* Öpik, 1967, p. 153, pl. 62, figs. 8–9; pl. 63, figs. 1, 3, holotype pygidium CPC 5908, paratypes CPC 5909–5911, 5913.
- **Pseudagnostus* cf. *idalis* Öpik, 1967, p. 154, pl. 63, fig. 4, CPC 5914.
- **Plethagnostus jarillensis* Rusconi, 1953, p. 4 [nom. nud.]; 1954, pp. 19–20, fig. 6, holotype pygidium NHMN 16674.
- **Pseudagnostus leptoplastorum* Westergård, 1944, p. 39, pl. 1, fig. 1, holotype pygidium SGU C459; also *P. leptoplastorum* Westergård sensu Ivshin, 1962, pp. 16–18, pl. 1, figs. 8–18, GMAN 646/105–107, 110, 113–117, 120, 124.
- **Pseudagnostus marginisulcatus* Kobayashi, 1962, p. 32, pl. III, figs. 10–11, holotype cephalon, paratype pygidium IGUT, unnumbered.
- **Pseudagnostus nuperus* Whitehouse, 1936, p. 100, pl. X, figs. 5–7, holotype cephalon UQ F3199, paratypes UQ F3200–3201.
- **Agnostus obtusus* Belt, 1868, pp. 10–11, pl. II, figs. 15–16 [fig. 15, not located, fig. 16 BMNH 58494].
- **Pseudagnostus primus* Kobayashi, 1935b, pp. 108–109, pl. XIV, figs. 6–10, IGUT, unnumbered (fig. 6 designated holotype cephalon); also Kobayashi, 1962, pp. 31–32, pl. III, figs. 15–17, pl. V, figs. 8–12, IGUT, unnumbered.
- Pseudagnostus pseudocyclopyge* Ivshin, 1956, pp. 17–19, pl. 1, figs. 1–8, 10, 16–17, holotype cephalon GMAN 74/926, paratypes GMAN 64/926, 66/926, 121/926, 70/926, 75/926, 83/926, 80/926, 77/926, 87/926, 86/926; Ivshin 1962, p. 18, pl. 1, figs. 19–22, GMAN 646/217, 646/125, 646/123.
- **Pseudagnostus sericatus* Öpik, 1967, pp. 152–153, pl. 62, fig. 7, holotype cephalon CPC 5907.
- **Pseudagnostus* sp. undet., Shergold in Shergold *et al.* 1976, pp. 264–265, pl. 41, figs. 9–11, NZAR 601–603.

The *cyclopyge* group possibly also includes:

- Pseudagnostus kobayashii* Wolfart, 1974, pp. 90–93, pl. 10, fig. 8; pl. 11, figs. 3–7, HAN 82/1, 82/2, 83/1, 84/2 (synonymy given).
- **Oedorhachis tennesseensis* Resser, 1938, p. 50, pl. 10, figs. 24–26, cotypes USNM 94871.
- **Pseudagnostus vastulus* Whitehouse, 1936, pp. 99–100, pl. X, figs. 3–4, holotype pygidium UQ F3203, paratype UQ F3202.
- Pseudagnostus* sp., Lu 1956b, pp. 367–368, pl. 1, figs. 1–2, ?IPP 8643–8644; also in Lu *et al.* 1965, p. 43, pl. 4, figs. 18–19, same repository and numbers.

Age and distribution. Late Cambrian: zones of *Parabolina spinulosa*, *P. brevispina*, *Leptoplastus raphidophorus*, and *Peltura scarabaeoides*, United Kingdom, Sweden; late Tuorian, *Glyptagnostus reticulatus* Zone; early Shidertan, *Irvingella* Zone, central Kazakhstan (Ivshin and Pokrovskaya 1968); Kushanian, *Blackwelderia paronai* fauna, Manchuria; late Kushanian, Afghanistan; Paishanian, *Chuangia* Zone, China (Kweichow), *Eochuangia* Zone, South Korea; late Mindyallan, *G. stolidotus* Zone, Idamean zones of *G. reticulatus* with *Proceratopyge nectans*, *Corynexochus plumula*, *Erixanium sentum*, and *Irvingella tropica* with *Agnostotes inconstans* (Öpik, 1963, 1967), western Queensland, Australia. Species of the group also occur in South America (Argentina), where their age is uncertain; in Antarctica (northern Victoria Land) of probable late Idamean age (Shergold *et al.* 1976); and possibly in North America (Tennessee), early Dresbachian, *Blountia* Zone (Resser 1938).

Comments. The *cyclopyge* group is heterogeneous and probably capable of further division. Its members exhibit some variation in shield shape, degree of effacement, orientation of anterior glabellar furrow, extent of pygidial pleural lobes, and strength, shape, and orientation of the pygidial spines. Early species are distinctly spectaculate, but later Cambrian ones may begin to approach the papilionate condition, in that the axial glabellar node migrates forwards and begins to interfere with the anterior furrow without actually coming to rest between the anterolateral lobes. The *cyclopyge* group grades with effacement into the *communis* group.

Securiger group (Pl. 15, fig. 13)

Nominal species. **Agnostus securiger* Lake, 1906, p. 20, pl. II, fig. 11, GSM 57650, late Cambrian, *Olenus* Zone, Outwood Shales, Chapel End, near Nuneaton, Warwickshire, U.K.

Diagnosis. Cephalon subovoid to subquadrate, *en grande tenue*, spectaculate, deliquiate marginal furrows, subovoid acrolobe, transverse rectilinear anterior glabellar furrow, median preglabellar furrow present. Pygidium subovoid to subrounded, *en grande tenue*, deliquiate marginal furrows, strongly deuterolobate, plethoid, posterolateral spines in advance of a line drawn across the rear of the deuterolobe plus a third sagittal spine developed from the posterior margin.

Other species. No other species are described, although a trispinose pygidium of pseudagnostid type is present in the *Elvinia* Zone assemblages of Cherry Creek, Egan Range, Nevada, U.S.A., USGS collection CO2527 (A. R. Palmer, pers. comm.).

Age and distribution. Late Cambrian: late *Olenus* Zone, Warwickshire, U.K.; early Franconian, *Elvinia* Zone, Nevada, U.S.A.

Comments. The generic name *Sulcatagnostus* was erected by Kobayashi (1937a, p. 451) for *Agnostus securiger* (see below). Apart from its possession of a third, sagittal, pygidial spine, *Sulcatagnostus securiger* (Lake) compares well with members of the *cyclopyge* group such as *Pseudagnostus ampullatus* Öpik and *P. idalis* Öpik, both of which have similar over-all morphology.

B. PAPILIONATE SPECIES GROUPS

Clarki group (Shergold 1975, p. 60) (Pl. 15, figs. 14–15)

Nominal species. **Pseudagnostus* (*Plethagnostus*) *clarki* Kobayashi, 1935a, p. 47, pl. IX, figs. 1–2, holotype pygidium USNM 93062, paratype USNM 146887, late Cambrian 'Briscoia' fauna, Hard Luck Creek, Alaska; refigured Palmer 1968, p. 29, pl. 15, figs. 10, 13–14.

Diagnosis. Cephalon subovoid to subcircular, effaced, wide borders with non-deliquiate marginal furrows, papilionate, V-form anterolateral glabellar furrows, median preglabellar furrow externally effaced, present parietally. Pygidium subovoid, effaced, wide borders with non-deliquiate marginal furrows, non-plethoid, weakly deuterolobate, small posterolateral spines sited well in advance of a transverse line drawn across the rear of the deuterolobe, nine to ten axial metameres.

Other species

**Pseudagnostus clarki maximus* Shergold, 1975, pp. 70–71, pl. 5, figs. 1–2, holotype cephalon CPC 11587, paratype CPC 11588.

**Pseudagnostus clarki patulus* Shergold, 1975, pp. 62–64, pl. 1, figs. 1–6, pl. 2, figs. 1–2, holotype cephalon CPC 11524, paratypes CPC 11525–11531.

**Pseudagnostus clarki prolatus* Shergold, 1975, pp. 64–69, pl. 3, figs. 1–6, pl. 4, figs. 1–6, holotype cephalon CPC 11532, paratypes CPC 11533–11542.

**Pseudagnostus cyclopygeformis* (Sun) *sensu* Kobayashi, 1933, pp. 97–98, pl. IX, figs. 19, 23–24, pl. X, fig. 7; 1935b, pp. 111–112, pl. III, figs. 12–14, IGUT no numbers.

**Pseudagnostus elix* Shergold, 1975, pp. 71–73, pl. 2, figs. 3–7, holotype pygidium CPC 11688, paratypes CPC 11689–11691.

**Pseudagnostus laevis* Palmer, 1955, pp. 97–98, pl. 19, figs. 8–9, 11–12, holotype pygidium USNM 123559, paratypes USNM 26990, 123560–123561.

- **Pseudagnostus orbiculatus* Shergold, 1975, pp. 73–74, pl. 12, figs. 8–12, holotype cephalon CPC 11591, paratypes CPC 11592–11595.
- **Pseudagnostus papilio* (*pars*) Shergold, 1972, pp. 28–31, pl. 1, fig. 2, CPC 8443, *non* pl. 1, figs. 1, 3–8, pl. 2, figs. 1–2 [*convergens* group].
- **Peronopsis planulata* Raymond, 1924, p. 395, pl. 12, fig. 9, holotype pygidium MCZ 1729.
- **Pseudagnostus* cf. *prolongus* (Hall and Whitfield) *sensu* Kindle and Whittington, 1965, p. 686, pl. 1, figs. 17–20, Kindle Collection.
- **Pseudagnostus* sp. II, Shergold 1972, p. 35, pl. 2, figs. 6–7, CPC 8458–8459.
- **Pseudagnostus* sp. III, Shergold 1972, pp. 35–36, pl. 2, fig. 8, CPC 8460.
- **Pseudagnostus* sp., Robison and Pantoja-Alor 1968, p. 780, pl. 97, figs. 17–18, USNM 158884–158885.

Possibly also belonging to this species group are:

Pseudagnostus α sp., Kobayashi 1935a, p. 41, plus plate explanation, pl. VIII, fig. 3, repository and number not known.

Pseudagnostus β sp., Kobayashi 1935a, p. 41, plus plate explanation, pl. VIII, fig. 4, repository and number not known.

Age and distribution. Late Cambrian: pre-Payntonian and Payntonian, *Rhaptagnostus clarki patulus* with *Caznaia squamosa* through *Neoagnostus quasibilobus* with *Tsinania nomas* Assemblage-Zones (Shergold 1975), western Queensland, Australia; Trempealeauan *Saukia* Zone, *Saukiella pyrene*? and *S. serotina* Subzones, Nevada, Montana, Vermont, Alaska, U.S.A.; Trempealeauan?, Oaxaca Province, Mexico; late Changshanian, *Kaolishania* Zone, Shantung, China; Fengshanian, *Tsinania* Zone, North and South Korea.

Comments. The *clarki* group is a homogeneous association of taxa exhibiting specific and subspecific variation in shapes and proportions, and border parameters.

Convergens group (Shergold 1975, p. 74) (Pl. 16, figs. 1–2)

Nominal species. **Pseudagnostus convergens* Palmer, 1955, pp. 96–97, pl. 19, figs. 14–15, holotype pygidium USNM 123562, paratype USNM 123563, late Cambrian, Trempealeauan, *Saukia* Zone, *Saukiella pyrene* Subzone, Nevada, U.S.A.

Diagnosis. Cephalon subovoid to subcircular, effaced and partially effaced, narrow borders with non-deliquate marginal furrows, papilionate, V-form anterolateral furrows, median prelabellar furrow externally effaced, present parietally. Pygidium subovoid, with rearwards converging flanks and acrolobe, narrow borders with non-deliquate marginal furrows, subplethoid, weakly deuterolobate, very small posterolateral spines well in advance of a transverse line drawn across the rear of the deuterolobe, ten late holaspisid metameres.

Other species

**Pseudagnostus bifax* Shergold, 1975, pp. 75–79, pl. 9, figs. 1–7, holotype cephalon CPC 11596, paratypes CPC 11597–11602, 11649, 11656, 11662, 11667–11668.

Aagnostus cyclopygeformis Sun, 1924, pp. 26–28, pl. II, fig. 1a–h, GSCh 501–504, 507–510; 1935, p. 16, pl. III, figs. 29–32, NUP 1194–1197; also **Pseudagnostus cyclopygeformis* (Sun) *sensu* Endo, 1939, p. 6, pl. 1, figs. 14–15, USNM 96092b–c, *non* fig. 13, USNM 96092a; *P. cyclopygeformis* (Sun) *sensu* Lu *et al.*, 1957, pl. 137, figs. 20–21, repository and numbers not known; 1965, p. 42, pl. 4, figs. 9–12, repository and numbers not known.

Pseudagnostus obsoletus Lermontova, 1951, pp. 10–11, pl. 2, figs. 8–10, repository and numbers unknown.

Pseudagnostus cf. *obsoletus* Lerm. (MS), Lermontova, 1940, p. 125, pl. 49, fig. 11, repository and number not known.

**Pseudagnostus papilio* Shergold, 1972, pp. 28–31, pl. 1, figs. 1, 3–8, *non* fig. 2 [*clarki* group], pl. 2, figs. 1–2, holotype cephalon CPC 8442, paratypes CPC 8443–8450; also 1975, pp. 79–82, pl. 11, figs. 1–8, CPC 11669–11677.

Possibly also belonging to this group is:

**Pseudagnostus* sp. I, Shergold 1972, p. 34, pl. 2, figs. 3–5, CPC 8457.

Age and distribution. Late Cambrian: pre-Payntonian, *Rhaptagnostus bifax* with *Neoagnostus denticulatus* and *R. clarki maximus* with *R. papilio* Assemblage-Zones (Shergold 1975), western Queensland, Australia; late Changshanian, *Kaolishania* Zone, Shantung, Hopei, China; Trempealeauan, *Saukiella pyrene* Sub-zone, *Saukia* Zone, Nevada, U.S.A.; Shidertan, *Lotagnostus trisectus/Peltura* Zone, Kazakhstan, U.S.S.R.

Comments. As for *clarki* group.

PSEUDAGNOSTID SPECIES UNASSIGNED

**Pseudagnostus* cf. *P. convergens* Palmer *sensu* Lochman, 1964, p. 51, pl. 13, fig. 10, USNM 140686.

Aagnostus cyclopyge Tullberg *sensu* Sun, 1935, pp. 15–16, pl. III, figs. 33–36, THU 1198–1201; *sensu* Lu *et al.* 1965, pp. 40–41, pl. 4, figs. 1–2 [reproductions of Sun's figures].

Pseudagnostus cyclopyge (Tullberg) *sensu* Wilson, 1954, p. 284, pl. 25, fig. 19, pl. 26, fig. 13.

*? *Hypagnostus empozadensis* Rusconi, 1953, p. 6 [*nom. nud.*]; 1954, pp. 34–35, pl. II, fig. 11, NHMM 16872, an effaced papilionate subquadrate cephalon.

* *Leiopyge empozadense* Rusconi, 1953, pp. 5–6 [*nom. nud.*]; 1954, pp. 33–34, pl. II, fig. 10, NHMM 16856, an incomplete pygidium.

* *Oedorhachis greendalensis* Resser, 1938, p. 51, pl. 10, fig. 9, USNM 94861.

* *Plethagnostus gyps* Clark, 1923, p. 124, pl. 1, fig. 9, holotype pygidium MCZ 1700; refigured Clark, 1924, p. 16, pl. 3, fig. 2; *sensu* Rasetti, 1944, p. 234, pl. 36, figs. 20–22, LU 1105a–c [may represent a distinct *en grande tenue* papilionate species group].

Pseudagnostus impressus Lermontova, 1940, p. 125, pl. 49, fig. 13, 13a, repository and numbers not known.

* *Pseudagnostus jeholensis* Kobayashi, 1951, pp. 76–77, pl. 7, figs. 13–14, IGUT no numbers; reproduced in Lu *et al.* 1965, p. 43, pl. 4, figs. 16–17.

Pseudagnostus josepha (Hall) as illustrated by: Frederickson 1949, p. 362, pl. 72, fig. 17, OGM 105-16F-53; Lochman 1950, pp. 329–330, pl. 46, fig. 14; Nelson 1951, p. 776, pl. 107, fig. 5; Bell *et al.* 1952, pp. 196–197, pl. 32, fig. 4a–b, pl. 33, fig. 1; Ellinwood 1953, p. 65, pl. 4, figs. 9–10; Wilson 1954, p. 284, pl. 25, figs. 5, 22.

* *Aagnostus maladensis* Meek, 1873, p. 464, USNM 24597 [a medley of taxa].

* *Pseudagnostus mesleri* (Resser) *sensu* Lochman, 1940, pp. 26–27, pl. 2, figs. 38–43, USNM 98703.

Microdiscus paronai Airaghi, 1902, p. 23, pl. 2, figs. 24–25, repository and numbers not known.

* *Spinagnostus pedrensis* Rusconi, 1951, pl. 8, fig. 9, NHMN 9963 [referred to *Leiopyge* by Rusconi 1953, p. 6, originally illustrated as a cephalon, this specimen is actually an indeterminate pseudagnostid pygidium].

Aagnostus pii Airaghi, 1902, p. 19, pl. 1, fig. 28, repository and number not known.

* *Pseudagnostus prolongus* (Hall and Whitfield) *sensu* Palmer, 1960, p. 61, pl. 4, figs. 5–6, USNM 136833a–b.

Pseudagnostus (*Rhaptagnostus*?) *semiovalis* Kobayashi, 1937a, pp. 452–453, pl. II, figs. 8–9, repository Freiburg, types destroyed (Kobayashi pers. comm., 1972).

? *Pseudagnostus* sp., Lu 1956a, pp. 282–283, pl. 1, fig. 8; Lu *et al.* 1965, p. 44, pl. 4, fig. 20, repository and number not known.

PSEUDAGNOSTI NOMINA NUDA

Pseudagnostus ovatus Rusconi, 1950, p. 94 [plate explanation error, fig. 6, for *P. parabolicus*].

Pseudagnostus huangluoensis Kobayashi, 1951, p. 75.

Pseudagnostus mirus Pokrovskaya in Vasilenko, 1963, p. 22, Chart 3 [listed].

Pseudagnostus solus Endo in Endo and Resser, 1937, p. 304 [listed].

DEFINITION OF GENERIC GROUPS

Since Jaekel erected *Pseudagnostus* in 1909 several attempts have been made to subdivide the genus, e.g. Clark 1923, Whitehouse 1936, Kobayashi 1937a, 1955, Lermontova 1940, *inter alia*. Accordingly there is a proliferation of generic and subgeneric names, some of which have doubtful taxonomic validity. These are briefly reviewed below in discussing the generic classification of pseudagnosti.

In this classification *Pseudagnostus* Jaekel, 1909, type species *Agnostus cyclopyge* Tullberg, 1880 (p. 26, pl. II, fig. 15a, c), is restricted to include only the *cyclopyge*, *communis*, and *bulgosus* species groups as documented above.

Plethagnostus, erected by Clark (1923, p. 124), originally differentially diagnosed from *Pseudagnostus* by having 'divergent dorsal [accessory] furrows continued to the border of the pygidium' as in *Plethagnostus gyps* Clark (1923, pl. I, fig. 9), its type species, is suppressed. This action is taken because:

Many pseudagnostid species are plethoid, the courses of the accessory furrows continuing to the marginal furrows, particularly in *en grande tenue* and partially effaced species groups, e.g. the *cyclopyge* and *communis* group referred above to *Pseudagnostus*; the type species is based on a single incomplete pygidium (MCZ 1700) which lacks a posterior margin; and usage of the name *Plethagnostus* has been confused by Kobayashi (1935a, pp. 46-47), who utilized Clark's taxon in a subgeneric sense for the species *Pseudagnostus clarki*, which has a papilionate cephalon and non-plethoid pygidium with effaced accessory furrows! Subsequent usage of *Plethagnostus* appears to have followed Kobayashi's interpretation. It is recommended that this practice be discontinued because the type specimen of *P. gyps* quite obviously does not belong to the same species group as *Pseudagnostus clarki*, and because of its incompleteness cannot be adequately classified anyway. *Plethagnostus gyps* Clark is left unclassified with respect to species groups and is referred to *Pseudagnostus s.l.*

Rhaptagnostus Whitehouse (1936, p. 97), based on *A. cyclopygeformis* Sun, 1924, was differentiated from *Pseudagnostus* by possessing 'an elliptical arrangement of foramina [notulae] in the post-axial region' of the pygidium, and a 'simple, non-spinose brim'. Sun's specimens (1924, pl. II, fig. 1a-h) appear to be parietal surfaces, and such surfaces of many pseudagnosti display notular lines given the right medium of preservation. The absence of pygidial spines in any pseudagnostid species is greatly doubted. Very often these spines are extremely small and readily destroyed by certain modes of preservation, e.g. in arenaceous matrices, and by negligent preparation. Cephalae matched by Sun with the pygidia which Whitehouse chose to differentiate from *Pseudagnostus*, are papilionate and thus different from those of *P. cyclopyge* (Tullberg), which is spectaculate. *P. cyclopygeformis* (Sun) is here included within the *convergens* species group. *Rhaptagnostus* is used herein to distinguish the two closely related papilionate species groups, *clarki* and *convergens*, from spectaculate ones at the generic level. This name is preferred to the previously and erroneously used *Plethagnostus* Clark *sensu* Kobayashi 1935a.

Sulcatagnostus was erected by Kobayashi (1937a, p. 451) for *A. securiger* Lake (1906, p. 20, pl. II, fig. 11), and distinguished by possessing 'irregular divergent furrows on the side lobes' (Kobayashi, 1937a, pp. 450-451). This was later redefined

as 'Pseudagnostinae with reticulated furrows on side lobes' (Kobayashi 1939, p. 159). The reticulation described (Pl. 15, fig. 13) refers to the caecal network of the cephalic acrolobe and pygidial pleural lobes. The presence of a caecal display, common on exfoliated specimens and thin exoskeletons under certain conditions of preservation, is itself insufficient to justify differentiation from *Pseudagnostus*. Overlooked by Kobayashi, however, is the fact that *A. securiger* Lake also possesses a trispinose pygidium (Rushton in Taylor and Rushton 1971, p. 20), which certainly is a significant characteristic. In view of the otherwise similar morphology to speculaculate pseudagnosti, *Sulcatagnostus* is retained as a subgenus of *Pseudagnostus*.

Euplethagnostus Lermontova (1940, p. 126), based on *E. subangulatus* Lermontova (1940, pl. XLIX, fig. 15, 15a), was compared to *Plethagnostus* Clark, 1923, but distinguished by the possession of posterolateral pygidial spines, sometimes an intranotular axis (lanceolate ridge), and the presence of a posterior pygidial terminal node. Such characteristics are emphatically not diagnostic in generic classification because: the type specimen of *P. gyps*, type species of *Plethagnostus*, is damaged and it is not possible to ascertain whether it possessed spines—Clark (1923) assumed that their traces were still apparent, and Rasetti (1944, pl. 36, figs. 20–22) has illustrated material possessing pygidial spines which can be assigned to *P. gyps*; the presence of terminal nodes and intranotular axes is commonly observed on a multiplicity of pseudagnostid parietal surfaces; and Lermontova's specimens are poorly illustrated and inadequately described, no type specimen was selected for *E. subangulatus* and the repository of material is unknown. *E. subangulatus* appears most similar to species classified herein with the *clavus* group. Its type specimens require redescription and re-illustration if the name *Euplethagnostus* is to be retained.

Problems associated with the taxonomic validation of *Pseudorhaptagnostus* Lermontova (1940, p. 126) have been previously discussed (Shergold 1972, p. 28). These problems remain unresolved. The name *Pseudorhaptagnostus* was introduced by Lermontova in 1940, *P. simplex* Lermontova (1951, pp. 12–13, pl. 2, figs. 11–17) being designated as type species. Although a second species, *P. punctatus* Lermontova, was illustrated in 1940, *P. simplex* was neither illustrated nor described until 1951. At this time a heterogeneous collection of cephalon and pygidia was figured. While the pygidia (Lermontova 1951, pl. 2, figs. 11–14) show morphological consistency, two types of cephalon were figured: one (fig. 15) is probably that associated with the pygidia, whereas the others (figs. 16–17) belong to a species of the *convergens* group. Nikitin (1956, pl. XIV, figs. 4–5) re-illustrated this combination of *convergens* group cephalon with *Pseudorhaptagnostus* pygidium. Such mismatching appears to result directly from Lermontova's failure to designate a holotype. According to Lermontova (1940), *Pseudorhaptagnostus* is differentiated from *Rhaptagnostus* Whitehouse in possessing a thickened pygidial rim and well-developed posterolateral spines. A lanceolate field [intranotular axis] is stated to be present on pygidial internal casts [parietal surfaces]. None of these characteristics is considered to justify separation from *Pseudagnostus*, either separately or in combination. Other characteristics exhibited by *Pseudorhaptagnostus simplex* can, however, be utilized if the name is to be retained (Shergold 1972, p. 28). These, which can only be verified from examination of the actual material on which *Pseudorhaptagnostus* is based, involve the cephalic and pygidial shapes, nature of their borders and pygidial spines, and pygidial seg-

mentation. Although it appears that *P. simplex* has much in common with the *clavus* species group recognized above, judgement on the validity of the genus must await clarification of the concept of the taxon. It is very likely that *Pseudorhaptagnostus* and *Euplethagnostus* Lermontova are synonyms. If so, *Pseudorhaptagnostus* has priority, being first listed.

Neoagnostus Kobayashi (1955, p. 473), type species *N. aspidoides* Kobayashi (1955, pp. 473–474), possesses a cephalon with trilobed glabella and median preglabellar furrow (Pl. 16, fig. 16). The holotype cephalon (Kobayashi 1955, pl. VII, fig. 5) is a parietal mould preserved *en grande tenue*. The associated pygidium (fig. 4), labelled paratype, is geragnostoid.

Hyperagnostus Kobayashi (1955, p. 474), based on *H. binodosus* Kobayashi (1955, p. 475), also has a trilobed glabella, but is said to differ from *Neoagnostus* in not possessing a median preglabellar furrow (Pl. 16, fig. 17). The holotype cephalon (1955, pl. VII, fig. 2) is partially exfoliated, somewhat distorted, and incomplete, the anterior portion of the cephalon having been lost. A thin veneer of exoskeleton lies across the position in which the median preglabellar furrow would be expected and its presence or absence cannot be absolutely verified; it appears not to be present on the external surface, but may be weakly present on the parietal surface. The assigned pygidium (1955, fig. 3) is agnostoid rather than pseudagnostoid. Although *Neoagnostus* and *Hyperagnostus* occur at different localities and are of slightly different ages, they are temporarily synonymized herein, *Neoagnostus* taking priority.

Machairagnostus Harrington and Leanza (1957, p. 63), based on *M. tmetus* Harrington and Leanza (1957, p. 64, fig. 7), is represented by parietal surfaces. The glabella is faintly trisegmented, but the cephalic acrolobe is scrobiculate. The pygidium is weakly deuterolobate, and the muscle-scar impressions of the third axial segment are incorporated into the anterior portion of the axis which is delineated by axial furrows. *M. tmetus* has the glabellar morphology of members of the *araneave-latus* species group, and pygidial characteristics of the *bilobus* group with which it is classified here. The scrobiculation of the cephalic acrolobe is non-diagnostic under the conditions of this classification, and so *Machairagnostus* is synonymized with *Neoagnostus*.

Pseudagnostina Palmer (1962, pp. 20–21), type species *P. contracta* Palmer (1962, pp. 20–21, pl. 2, figs. 18–20, 22–25), was coined for pseudagnosti having 'Peronopsis-like cephalon and *Pseudagnostus*-like pygidium'. The concept of the taxon is broadened somewhat here by the inclusion of some Asian species previously referred to *Agnostus douvillei* Bergeron, 1899. Because of over-all basic similarity of the pygidium to that of other pseudagnosti, *Pseudagnostina* is regarded here as a subgenus of *Pseudagnostus*—effaced and partially effaced, strongly spectaculate, weakly deuterolobate species constituting the *contracta* species group.

SUMMARY

Spectaculate species groups fall readily into two larger groupings:

1. The *bulgosus-communis-contracta-cyclopyge-securiger* grouping whose morphology differs by degree and which can largely be encompassed within a concept of *Pseudagnostus* based on its type species *P. cyclopyge* (Tullberg 1880). Effaced

variants are differentiated as the *contracta* group regarded as a distinct subgenus, *Pseudagnostina* Palmer, 1962; and the *securiger* group, with three pygidial spines, likewise is separated at the subgeneric level as *Sulcatagnostus* Kobayashi, 1937a.

2. The *araneavelatus-bilobus-canadensis-clavus* grouping is united by an arrangement of glabellar lobation and furrowing different from that of *Pseudagnostus*. The anterolateral lobes are closer together and may meet adaxially so that the glabellar furrows intersect as a cross. Within this division species groups are differentiated by shield shape, and degree of effacement, particularly by which glabellar furrows are effaced and which are not. Five generic names appear to be available for classifying these groups: *Pseudorhaptagnostus* Lermontova, 1940; *Euplethagnostus* Lermontova, 1940; *Neoagnostus* Kobayashi, 1955; *Hyperagnostus* Kobayashi, 1955; and *Machairagnostus* Harrington and Leanza, 1957. As indicated above, *Pseudorhaptagnostus* and *Euplethagnostus* may be synonyms, the former taking priority; and *Hyperagnostus* and *Machairagnostus* are regarded as synonyms of *Neoagnostus*.

Although *Pseudorhaptagnostus* and *Euplethagnostus* have priority over *Neoagnostus*, their concepts are very poorly understood, and it has been found not possible to obtain adequate information to verify their characteristics. Accordingly, *Neoagnostus* is temporarily adopted in this classification, in preference to either of the Russian genera, for the *araneavelatus-bilobus-canadensis-clavus* grouping.

The papilionate species groups, *clarki* and *convergens*, are placed here in *Rhaptagnostus* Whitehouse, 1936, because its interpretable type species is representative of the *convergens* group.

Thus the following classification is adopted:

Family Diplagnostidae Whitehouse, 1936, emend. Öpik, 1967.

Subfamily Pseudagnostinae Whitehouse, 1936.

Genus *Pseudagnostus* Jaekel, 1909.

Type species: *Agnostus cyclopyge* Tullberg, 1880 (designated Jaekel, 1909). Pseudagnostinae with long (sag.) anteriorly rounded or pointed anterior glabellar lobe, axial node lying behind anterolateral lobes and anterior furrow which is straight or curved rearwards sagittally. Shields are subcircular to subovoid, effaced to *en grande tenue*, non-deliquate to deliquate, weakly to strongly deuterolobate. Up to eight late holaspis pygidial metameres.

Subgenus *Pseudagnostus* Jaekel, 1909.

Type species and diagnosis as above.

Group *bulgosus*, based on *Pseudagnostus bulgosus* Öpik, 1967.

Group *communis*, based on *Agnostus communis* Hall and Whitfield, 1877.

Group *cyclopyge*, based on the type species.

Subgenus *Pseudagnostina* Palmer, 1962.

Type species: *Pseudagnostina contracta* Palmer, 1962 (by original designation). Spectaculate Pseudagnostinae with subquadrate shields and with effaced median preglabellar furrow, accessory furrows, and deuterolobe.

Group *contracta*, based on the type species.

Subgenus *Sulcatagnostus* Kobayashi, 1937a.

Type species: *Agnostus securiger* Lake, 1906 (designated Kobayashi, 1937a). Spectaculate *en grande tenue* Pseudagnostinae with trispinose pygidium.

Group *securiger*, based on the type species.

Genus *Neoagnostus* Kobayashi, 1955.

Type species: *Neoagnostus aspidoides* Kobayashi, 1955 (by original designation). Spectaculate Pseudagnostinae with anterolateral glabellar lobes close together or meeting adaxially, and a tendency to efface or over-deepen either the furrows in front of or behind the anterolateral lobes; anterior lobe small and rhomboid. Pygidium with distinct tendency to incorporate a third segment into that portion of the axis defined by axial furrows; retrol spines. Generally, species have subquadrate shields, whose external morphology may be effaced, partially effaced or *en grande tenue*, non-deliquiate to deliquiate, weakly to strongly deuterolobate. Up to eight late holaspide pygidial metameres.

Group *araneavelatus*, based on *Pseudagnostus araneavelatus* Shaw, 1951.

Group *bilobus*, based on *Pseudagnostus bilobus* Shaw, 1951.

Group *canadensis*, based on *Aagnostus canadensis* Billings, 1860.

Group *clavus*, based on *Pseudagnostus clavus* Shergold, 1972.

Genus *Rhaptagnostus* Whitehouse, 1936.

Type species: *Aagnostus cyclopygeformis* Sun, 1924 (designated Whitehouse, 1936). Papilionate Pseudagnostinae with subovoid shields, externally generally effaced or partially effaced. Pygidia with ten late holaspide metameres; spines advanced with respect to the rear of the deuterolobe, and minute.

Group *clarki*, based on *Pseudagnostus clarki* Kobayashi, 1935a.

Group *convergens*, based on *Pseudagnostus convergens* Palmer, 1955.

Non-investigated genera of Pseudagnostinae are *Litagnostus* Rasetti, 1944, *Xestagnostus* Öpik, 1967, and *Oxyagnostus* Öpik, 1967.

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APPENDIX A

MORPHOLOGICAL CONDITIONS APPLICABLE TO PSEUDAGNOSTI

Constricted/unconstricted acrolobes. If the lateral margins of the acrolobe are curved slightly inwards, then the condition is known as constricted (Öpik 1967). Where a constant curvature of the flanks of the acrolobe is maintained the condition is said to be unconstricted. Most species of *Pseudagnostus* have constricted pygidial acrolobes, the condition being most readily observed on parietal surfaces. Some species also have constricted cephalic acrolobes.

Deliquiate/non-deliquiate marginal furrows. Marginal furrows which are deeply grooved or channel-like are described as deliquiate (Shergold 1975). If the marginal furrow is merely a break in convexity at the junction of the acrolobe and border the condition exhibited is non-deliquiate. Gradations exist, for which the term subdeliquiate is introduced to permit the description of degrees of deepening of furrows. Degree of deliquiation is related directly to degree of effacement. Exoskeleton and mould of the same specimen will have differing degrees of deliquiation, the mould having deeper, wider furrows.

Deuterolobate. All pseudagnosti are deuterolobate. Degree of elevation of the deuterolobe, however, varies. *En grande tenue* species generally have a tumid deuterolobe well defined by accessory furrows. For this condition the term strongly deuterolobate is used here. Species with depressed deuterolobes are described as weakly deuterolobate.

Effaced/effacement/partial effacement. An effaced condition is one in which furrows and lobes with visible convexity are obliterated to give a smooth or nearly smooth surface. In Pseudagnostinae all conditions of partial effacement exist, from highly effaced to *en grande tenue*.

En grande tenue. Introduced by Öpik (1961b, p. 55), this term was redefined (Öpik 1967, p. 56) to categorize agnostids having distinct lobes and furrows.

Papilionate. Pseudagnostinae in which the axial glabellar node lies between the anterolateral lobes are termed papilionate. The term is derived from the butterfly-like appearance of these lobes and furrows (Shergold 1975, p. 42).

Plethoid. Pseudagnostinae with accessory furrows clearly encircling the deuterolobe or continued posteriorly to the marginal furrow exhibit a plethoid condition (Shergold 1972, p. 15).

Retral. This term refers to the siting of the posterolateral pygidial spines at the rear of the shield, behind or at the level of the rear of the deuterolobe.

Simplicimarginate/zonate borders. Simplicimarginate agnostids have a basic unmodified border. Those having a duplicated posterior margin are said to be zonate (Öpik 1967, p. 61).

Spectaculate. A term introduced for pseudagnosti in which the axial glabellar node lies to the rear of the anterolateral glabellar lobes, and is therefore also to the rear of the anterior glabellar furrow. The resulting appearance resembles a bespectacled face—hence the term (Shergold 1975, p. 42).

APPENDIX B

CLASSIFICATION OF SPECIES ASSIGNABLE TO *PSEUDAGNOSTUS sensu lato*

Species/Author/Date	Original Generic Assessment	Species Group	Revised Generic Assignment
1. <i>acutifrons</i> Troedsson, 1937	<i>Rhaptagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>
2. cfr. <i>acutus</i> Kobayashi, 1938	<i>Homagnostus</i>	<i>clavus?</i>	<i>Neoagnostus</i>
3. <i>ampullatus</i> Öpik, 1967	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
4. <i>angustilobus</i> Ivshin, 1956	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
5. <i>araneavelatus</i> Shaw, 1951	<i>Pseudagnostus</i>	<i>araneavelatus</i>	<i>Neoagnostus</i>
6. <i>aspidoides</i> Kobayashi, 1955	<i>Neoagnostus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
7. <i>bifax</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>convergens</i>	<i>Rhaptagnostus</i>
8. <i>bilobus</i> Shaw, 1951	<i>Pseudagnostus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
9. <i>binodosus</i> Kobayashi, 1955	<i>Hyperagnostus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
10. <i>bituberculatus</i> Ivshin, 1960	<i>Pseudagnostus</i>	<i>clavus?</i>	<i>Neoagnostus</i>
11. <i>boltonensis</i> Resser, 1938	<i>Oedorhachis</i>	<i>bulgosus</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
12. <i>bulgosus</i> Öpik, 1967	<i>Pseudagnostus</i>	<i>bulgosus</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
13. <i>canadensis</i> Billings, 1860	<i>Agnostus</i>	<i>canadensis</i>	<i>Neoagnostus</i>
14. <i>cavernosus</i> Rosova, 1960	<i>Pseudagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>
15. <i>chinensis</i> Dames, 1883 (<i>pars</i>)	<i>Agnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
16. <i>clarki</i> Kobayashi, 1935a	<i>Plethagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
17. <i>clarki patulus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
18. <i>clarki prolatus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
19. <i>clarki maximus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
20. <i>clavus</i> Shergold, 1972	<i>Pseudagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>
21. <i>coloradoensis</i> Shumard, 1961	<i>Agnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
22. <i>communis</i> Hall and Whitfield, 1877	<i>Agnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)

Species/Author/Date	Original Generic Assessment	Species Group	Revised Generic Assignment
23. <i>contracta</i> Palmer, 1962	<i>Pseudagnostina</i>	<i>contracta</i>	<i>Pseudagnostus</i> (<i>Pseudagnostina</i>)
24. <i>convergens</i> Palmer, 1955	<i>Pseudagnostus</i>	<i>convergens</i>	<i>Rhaptagnostus</i>
25. <i>convexus</i> Chu, 1959 (<i>pars</i>)	<i>Homagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
26. <i>coronatus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>araneavelatus</i>	<i>Neoagnostus</i>
27. <i>cyclopyge</i> Tullberg, 1880	<i>Aagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
28. <i>cyclopygeformis</i> Sun, 1924	<i>Aagnostus</i>	<i>convergens</i>	<i>Rhaptagnostus</i>
29. <i>cyclostigma</i> Raymond, 1924	<i>Phalacroma</i>	<i>araneavelatus</i>	<i>Neoagnostus</i>
30. <i>denticulatus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>araneavelatus</i>	<i>Neoagnostus</i>
31. <i>douvillei</i> Bergeron, 1899	<i>Aagnostus</i>	<i>contracta</i>	<i>Pseudagnostus</i> (<i>Pseudagnostina</i>)
32. <i>elix</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
33. <i>empozadense</i> Rusconi, 1954	<i>Lejopyge</i>	?	?
34. <i>empozadensis</i> Rusconi, 1954	<i>Hypagnostus</i> ?	?	?
35. <i>greeudalensis</i> Resser, 1938	<i>Oedorhachis</i>	?	?
36. <i>gyps</i> Clark, 1923	<i>Plethagnostus</i>	?	?
37. <i>huangluosensis</i> Kobayashi, 1966	<i>Pseudagnostus</i>		<i>nomen nudum</i>
38. <i>idalis</i> Öpik, 1967	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
39. <i>impressus</i> Lermontova, 1940	<i>Pseudagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
40. <i>jauei</i> Clark, 1923	<i>Aagnostus</i>	<i>canadensis</i>	<i>Neoagnostus</i>
41. <i>jarillensis</i> Rusconi, 1953	<i>Plethagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
42. <i>jeholensis</i> Kobayashi, 1951	<i>Pseudagnostus</i>	?	?
43. <i>josepha</i> Hall, 1863	<i>Aagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
44. <i>kobayashii</i> Wolfart, 1974	<i>Pseudagnostus</i>	<i>cyclopyge</i> ?	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
45. <i>koerferi</i> Monke, 1903	<i>Aagnostus</i>	<i>contracta</i>	<i>Pseudagnostus</i> (<i>Pseudagnostina</i>)
46. <i>laevis</i> Palmer, 1955	<i>Pseudagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
47. <i>latus</i> Kobayashi, 1938	<i>Pseudagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
48. <i>leptoplastorum</i> Westergård, 1944	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
49. <i>levatus</i> Romanenko, 1967	<i>Pseudagnostus</i>	<i>bulgosus</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
50. <i>longicollis</i> Kobayashi, 1966	<i>Pseudagnostus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
51. <i>maladensis</i> Meek, 1873	<i>Aagnostus</i>	?	?
52. <i>marginisulcatus</i> Kobayashi, 1962	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
53. <i>mesleri</i> Resser, 1938	<i>Oedorhachis</i>	<i>bulgosus</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
54. <i>mestus</i> Öpik, 1967	<i>Pseudagnostus</i>	<i>bulgosus</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
55. <i>mirus</i> Pokrovskaya, 1963	<i>Pseudagnostus</i>		<i>nomen nudum</i>
56. <i>neoi</i> Hall and Whitfield, 1877	<i>Aagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
57. <i>nganasanicus</i> Rosova, 1964	<i>Pseudagnostus</i>	<i>bulgosus</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
58. <i>nuperus</i> Whitehouse, 1936	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
59. <i>obsoletus</i> Lermontova, 1951	<i>Pseudagnostus</i>	<i>convergens</i>	<i>Rhaptagnostus</i>
60. <i>obtus</i> Belt, 1868	<i>Aagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
61. <i>orbiculatus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
62. <i>orientalis</i> Kobayashi, 1933	<i>Pseudagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
63. <i>ovatus</i> Rusconi, 1950	<i>Pseudagnostus</i>		<i>nomen nudum</i>
64. <i>papilio</i> Shergold, 1971	<i>Pseudagnostus</i>	<i>convergens</i>	<i>Rhaptagnostus</i>
65. <i>paronai</i> Airaghi, 1902	<i>Microdiscus</i>	?	?
66. <i>pedtensis</i> Rusconi, 1951	<i>Spinagnostus</i>	?	?
67. <i>pui</i> Airaghi, 1902	<i>Aagnostus</i>	?	?
68. <i>planulata</i> Raymond, 1924	<i>Peronopsis</i>	<i>clarki</i>	<i>Rhaptagnostus</i>
69. <i>primus</i> Kobayashi, 1962	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
70. <i>priscus</i> Kobayashi, 1955	<i>Trinodus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
71. <i>prolongus</i> Hall and Whitfield, 1877	<i>Aagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
72. <i>pseudocyclopyge</i> Ivshin, 1956	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
73. <i>punctatus</i> Lermontova, 1940	<i>Pseudagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>
74. <i>quadratus</i> Lazarenko, 1966	<i>Pseudagnostus</i>	<i>clavus</i> ?	<i>Neoagnostus</i>
75. <i>quasibilobus</i> Shergold, 1975	<i>Pseudagnostus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
76. <i>rotundatus</i> Lermontova, 1940	<i>Pseudagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
77. <i>securiger</i> Lake, 1906	<i>Aagnostus</i>	<i>securiger</i>	<i>Pseudagnostus</i> (<i>Sulcatagnostus</i>)
78. <i>semiovalis</i> Kobayashi, 1937a	<i>Rhaptagnostus</i>	?	?
79. <i>sentosus</i> Grant, 1965	<i>Pseudagnostus</i>	<i>communis</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
80. <i>sericatus</i> Öpik, 1967	<i>Pseudagnostus</i>	<i>cyclopyge</i>	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
81. <i>simplex</i> Lermontova, 1951	<i>Pseudorhaptagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>

Species/Author/Date	Original Generic Assessment	Species Group	Revised Generic Assignment
82. <i>solus</i> Endo, 1937	<i>Pseudagnostus</i>		nomen nudum
83. <i>subangulatus</i> Lermontova, 1940	<i>Euplethagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>
84. <i>tennesseensis</i> Resser, 1938	<i>Oedorhachis</i>	<i>cyclopyge</i> ?	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
85. <i>metus</i> Harrington and Leanza, 1957	<i>Machairagnostus</i>	<i>bilobus</i>	<i>Neoagnostus</i>
86. <i>vastulus</i> Whitehouse, 1936	<i>Pseudagnostus</i>	<i>cyclopyge</i> ?	<i>Pseudagnostus</i> (<i>Pseudagnostus</i>)
87. <i>vicaria</i> Āpik, 1967	<i>Pseudagnostus</i>	<i>contracta</i>	<i>Pseudagnostus</i> (<i>Pseudagnostina</i>)
88. <i>vulgaris</i> Rosova, 1960	<i>Pseudagnostus</i>	<i>clavus</i>	<i>Neoagnostus</i>

TWO NEW BAJOCIAN MICROCONCH OTOITID AMMONITES AND THEIR SIGNIFICANCE

by C. F. PARSONS

ABSTRACT. Two new Bajocian (Middle Jurassic), microconch species belonging to the ammonite family Otoitidae, *Trilobiticeras* (*Trilobiticeras*) *cricki* nov. and *Emileia* (*Otoites*) *douvillei* nov., are described, and are paired with their probable macroconch partners, *T. (Emileites)* *malenotatus* (Buckman) and *E. (E.) subcadiconica* Buckman respectively. The stratigraphic distribution of the main members of the subfamily Otoitinae in southern England shows that the two new species fill an important gap in our knowledge of this subfamily. In particular *T. (T.) cricki* is of fundamental importance, as it is the undoubted ancestor to both *Emileia* and *Frogdenites* and possibly also *Pseudotoites*. With their restricted stratigraphic range and wide geographic distribution, these new species are valuable stratigraphic indices for delimiting the base of the *ovalis* Subzone of the *laeviuscula* Zone. The most important exposures of the *ovalis* Subzone are discussed and the famous fauna described from the south of France by Douville is revised.

DURING the course of a recent stratigraphic study of the Bajocian rocks (Middle Jurassic) of southern England (Parsons 1974, pp. 164–171), large ammonite collections have been made from some long-neglected horizons. In particular the *ovalis*, or so called ‘Lower white iron-shot’ bed of Dundry Hill, near Bristol (Buckman and Wilson 1896, pp. 708–709, table iv), has yielded an interesting assemblage, which may be correlated with the *ovalis* Subzone of the *laeviuscula* Zone (Parsons 1974, p. 169)—see Table 1 for the zonal scheme used here. The majority of ammonites

TABLE 1. Zones and relevant subzones of the Lower Bajocian substage (= Middle Bajocian *sensu* Arkell 1956), after Parsons 1974.

	ZONES	SUBZONES
LOWER BAJOCIAN	<i>Stephanoceras humphriesianum</i>	
	<i>Emileia (Otoites) sauzei</i>	
	<i>Witchellia (Witchellia) laeviuscula</i>	<i>W. (W.) laeviuscula</i>
	<i>Hyperhoceras discites</i>	<i>Sonninia ovalis</i>

collected from this horizon (+56%), belong to the *Witchellia*/*Pelekodites* dimorphic group. However, intensive collecting revealed that a small proportion of the total fauna consists of two, as yet undescribed, species belonging to the microconch subgenera *Otoites* and *Trilobiticeras*. A study of the previous literature and pre-existing museum collections showed that these stratigraphically important species had been collected and recognized as distinct for some considerable time; it has merely taken a hundred years for them to be formally described. The small physical size of these two new microconch species, as well as their relative rarity in comparison with the abundant *Witchellia*, goes some way towards explaining their absence in previous works on the Bajocian Otoitidae (Westermann 1954).

As already noted, these two new species form only a minor part of the total ammonite fauna of this age in England. However, at comparable horizons in southern Europe the sonninid ammonites are less dominant, whilst the stephanoceratids are relatively more abundant. It is thus not surprising that this area of Europe has produced the majority of previous records of these two new species, particularly the south of France, Portugal, and Sicily. With their wide geographic distribution and relatively restricted stratigraphic range, these ammonites are of great value for correlation purposes, particularly for between sonninid-dominated north-west Europe and the Tethyan region. These taxa are also of considerable phylogenetic importance, as they form a critical link between the early stephanoceratids of the *concaum/discites* Zones and the more abundant forms of the upper *laeviuscula/sauzei* Zones. As *Emileia* (*Otoites*) *douvillei* nov. and *Trilobiticeras* (*Trilobiticeras*) *cricki* nov. are characteristic of the *ovalis* Subzone of the *laeviuscula* Zone, some discussion of the stratigraphy of this horizon in southern England and elsewhere in Europe is given.

Numbers preceded by these abbreviations refer to ammonites in the following collections:

BMNH.	The British Museum (N.H.), London.
Cb.	Bristol City Museum.
IGS.	The Institute of Geological Sciences, London.
M.	The École des Mines Collection, Université de Paris-Sud, Paris.
OUM.	The Oxford University Museum.
SM.	The Sedgwick Museum, Cambridge.
CP.	The author's collection, Liverpool University.

Under type species M = macroconch and m = microconch.

SYSTEMATIC DESCRIPTIONS

Class CEPHALOPODA

Subclass AMMONOIDEA

Superfamily STEPHANOCERATACEA Neumayr, 1875

Family OTOITIDAE Mascke, 1907

The classification of the Otoitidae follows Westermann (1964), who divided this family between two subfamilies, the Otoitinae and Sphaeroceratinae.

Subfamily OTOITINAE Mascke, 1907

The generic classification within this subfamily follows Westermann (1964, pp. 51–54), except for the inclusion of *Frogdenites*, which on both morphological and stratigraphic criteria has been transferred from the Sphaeroceratinae.

Genus *Emileia* Buckman, 1898

Type species. Emileia (*Emileia*) *brocchii* (J. Sowerby, 1818), (M.).

Diagnosis. A group of macroconch and microconch, sphaeroconic ammonites, which on the inner whorls bear 'club'-shaped primary ribs, terminated by blunt nodes, from which divide two or more rounded secondary ribs. The nominate subgenus consists of medium to large-sized macroconch ammonites, with a terminal constriction and flared-mouth border, and which vary from involute sphaerocones via cadicones to evolute platycones.

Subgenus *Otoites* Mascke, 1907

Type species. Emileia (Otoites) sauzei (d'Orbigny, 1846), (m.).

Diagnosis. A group of moderately small sized, lappeted microconch ammonites, which are characteristically involute sphaerocones, with a pronounced contraction of the body chamber. The ribbing style on the inner whorls is identical to its macroconch, *Emileia s. str.*, that is 'club'-shaped primary ribs, dividing into three to four finer secondaries. On its outer whorls, *Otoites* tends to develop sharp tubercles or spines at this point of division, whilst on the body chamber the secondary ribs tend to become inflated and coarsened, often with an alternation of strength on the last half whorl, with every second, third, or fourth rib being more inflated than its neighbour.

Emileia (Otoites) douvillei sp. nov.

Plate 17, figs. 6, 7, and 9; text-fig. 1

- 1885 *Sphaeroceras sauzei* d'Orbigny; Douvillé *non* d'Orbigny, p. 41, pl. III, fig. 9a-b.
 ?1921 *Otoites sauzei*; Riche and Roman *non* d'Orbigny, p. 138, pl. 6, fig. 8.
 1925 *Sphaeroceras (Otoites) sauzei* d'Orbigny; Renz *non* d'Orbigny, p. 32, pl. 11, fig. 8 and 8a.
 ?1929 *Emileia sauzei* d'Orbigny; Lanquine *non* d'Orbigny, p. 293, pl. ix, fig. 6.
 1960 *Otoites* sp. (*O. sauzei* Roman *non* d'Orbigny); Lelièvre, p. 17.
 1960 *Otoites* sp.; Dubar, p. 52, pl. vii, figs. 25-26 and ?24.
 1961 *Otoites* cf. *sauzei* (d'Orbigny) (Douvillé, 1885, pl. 3, fig. 9); Ruget-Perrot, p. 54.
 ?1967 *Otoites* sp.; Gabilly and Rioult, p. 3.
 ?1974 *Emileia (Otoites)* sp. nov.; Parsons, p. 168.
 ?1975 *Emileia (Otoites)* sp. nov.; Morton, pp. 84-85, pl. 16, figs. 5-6.
non 1954 *Otoites fortis* n. sp.; Westermann, pp. 103-106, pl. 3, figs. 2-4; text-figs. 10 and 21.

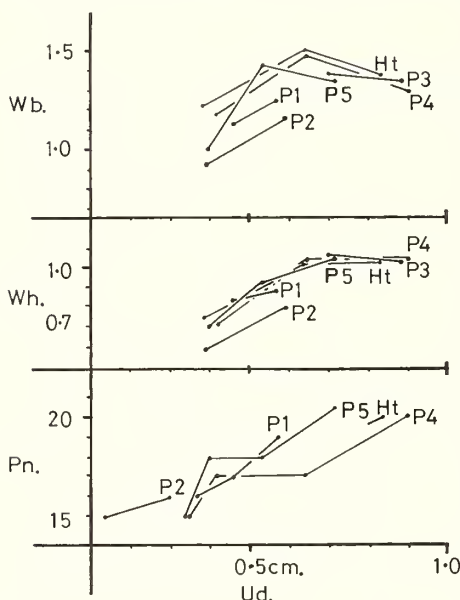
Material. Two specimens — 0.30 m from the top of bed 2, Barns Batch Spinney (National Grid Reference ST 557659), Dundry Hill, Bristol (Buckman and Wilson 1896, p. 689), BMNH. C79428-79429; five Dundry specimens from old museum collections, BMNH. C75242, IGS. 25189, Cb. 4744, Cb. 4957-4958, and one specimen + 0.30 m from the base of bed 4, Bruton Railway quarry (ST 682 345), Bruton, Somerset (Richardson 1916, p. 495), BMNH. C79432, a total of eight specimens.

Dimensions. Holotype, Cb. 4744, from Dundry Hill, and by matrix from the *ovalis* bed. It is complete, with the base of lappets, and just over three-quarters of a whorl of body chamber at a maximum diameter of 2.67 cm.

Diameter (D)	Umbilical diameter (Ud)	Number of primary ribs (Pn)	Whorl height (Wh)	Whorl breadth (Wb)	$\frac{Wb}{Wh}$
2.50	0.83 (33%)	c. 20	1.04 (42)	1.36 (54)	1.31
2.16	0.64 (30)	—	1.01 (47)	1.50 (69)	1.49
First paratype, BMNH. C79429, with a quarter whorl of body chamber.					
1.96	0.57 (29)	19	0.89 (45)	1.25 (64)	1.4
1.7	0.46 (27)	17	0.84 (49)	1.13 (67)	1.35
Second paratype, BMNH. C79428.					
1.7	0.59 (35)	—	0.8 (47)	1.15 (68)	1.44
1.31	0.39 (30)	—	0.6 (46)	0.92 (70)	1.53

Description. A small (c. 2.3-2.7 cm diameter), sphaeroconic ammonite, with a strongly contracted body chamber, which extends for three-quarters to one whorl. The prorsiradiate primary ribs are short, blunt, and expand into 'club'-shaped nodes at

the point of division into three to four secondary ribs. These secondaries are relatively coarse, rounded rather than sharp, and bend forward only slightly over the rounded venter. The primary ribs weaken on the body chamber, whilst the secondaries, particularly on the last quarter whorl, are reduced to two per primary, and become



TEXT-FIG. 1. A plot of whorl breadth (Wb), whorl height (Wh), and number of primary ribs (Pn), against umbilical diameter (Ud), for *Emileia (Otoites) douvillei* sp. nov. Ht = holotype; P = paratype.

inflated and coarsened, often with a tendency to become irregularly swollen. Thus on the last half whorl of the third paratype (IGS. 25189), every second or third rib is more expanded than its neighbour. The relative primary rib density increases rapidly (see text-fig. 1), from 15 to 16 per whorl on the inner whorls, to 20 to 21 on the body chamber. There is very little relative change in whorl cross-section, which stays more or less rounded, but depressed throughout ontogeny. The exception to this is found on the last quarter whorl of the body chamber, where, associated with the rapid uncoiling of the umbilical seam, there is a marked decline in whorl breadth (Wb), relative to whorl height (Wh)—see text-fig. 1. This rapid uncoiling of the body chamber changes the shell shape from a slightly sphaeroconic, to a more evolute form, although it is never as evolute as *Trilobiticerus (T.) cricki* nov. The mouth border is characterized by a pair of spatulate lappets, which extend from the mid-whorl position (see Pl. 17, fig. 6a).

Type series (six specimens). The holotype (Pl. 17, fig. 6a–b), the best-preserved British

specimen, comes from an old collection in the Bristol City Museum (Cb. 4744). The matrix of this specimen is identical to that of bed 2, Barns Batch Spinney, Dundry (Buckman and Wilson 1896, p. 689); that is, the *ovalis* bed, which is unique to the west side of Dundry Hill. The first paratype (BMNH. C79429), has only a quarter whorl of body chamber, but it is clearly very similar to the holotype in both proportions and ornament (see Pl. 17, fig. 9a–b), and like the second paratype (BMNH. C79428), it was collected *in situ* from bed 2, Barns Batch Spinney, Dundry, thus confirming the type horizon of the holotype. The third paratype (IGS. 25189), has the best-preserved lappets, whilst the fourth is a well-preserved specimen (Cb. 4957), which is recorded on its label as coming from the 'Sherborne district' of north Dorset. However, the matrix of this specimen, which is totally atypical of the Sherborne area, would suggest a true provenance from the *ovalis* bed of Dundry. Lastly the fifth paratype (BMNH. C75242), is another well-preserved specimen, with a matrix characteristic of the *ovalis* bed (Pl. 17, fig. 7a–b).

Sexual dimorphism. Sexual dimorphism is well marked in this group. *Emileia (Otoites) douvillei* nov., like other members of this subgenus, shows typical microconch

features. The mature shell is of relatively small size, and exhibits well-developed lappets. The corresponding macroconch is less well represented in the *ovalis* bed. A typical specimen from Dundry, *ex* Etheridge Collection, BMNH. C75279, is an involute, slightly cadiconic form, with bullate primary ribs and a quarter of a whorl of body chamber at a diameter of 4.1 cm, see Plate 17, fig. 8. The matrix of this specimen suggests the *ovalis* bed as its source. This is confirmed by the occurrence of a complete specimen, with a plain mouth band, 9.0 cm in diameter, from the *ovalis* bed of West Dundry (Bristol University, Department of Geology, No. 67). These macroconchs are best referred to *E. (E.) subcadiconica* S. Buckman (1927, in 1909–1930, pl. 711). The type specimen of the latter (IGS. 49304), although fragmentary and wholly septate, exhibits, as noticed by Buckman (*loc. cit.*), a typical *ovalis* bed matrix.

Stratigraphic range. *E. (O.) douvillei* appears to be characteristic of the *ovalis* Subzone of the *laeviuscula* Zone. However, this taxon probably ranges up into the base of the *laeviuscula* subzone, although the specimens referred to it from the basal part of the 'Sandford Lane fossil bed', near Sherborne, Dorset (ST 628 179), are possibly not conspecific. The latter are slightly larger, with a different primary rib density (= *Otoites* sp. nov.; Parsons 1974, p. 168). By way of comparison, a single specimen from this locality and horizon, in the Reed Collection of the Yorkshire Museum is figured here (Pl. 17, fig. 4).

Geographic range. Apart from Dundry Hill, and more doubtfully Sandford Lane, the only other British localities to yield this species are Bruton Railway quarry, Bruton, near Castle Cary, Somerset (Richardson 1916, p. 495, bed 4), which has yielded one specimen, BMNH. C79432, and possibly Berreraig Burn, Isle of Skye, Scotland (= *Otoites* sp. nov.; Morton 1975, pl. 16, figs. 5 and 6). It is impossible to be certain of the latter, as the specimen is not well preserved and is badly localized. Elsewhere this species has been recorded from the south of France (Douville 1885; Lanquine 1929), Sicily (Renz 1925), Portugal (Ruget-Perrot 1961), and Morocco (Dubar 1960).

Discussion. As may be seen from the synonymy list, the presence of this species has been noted by numerous authors, most of whom commented on its distinctive nature. This species has been named in honour of H. Douville, who was the first to figure it (Douville 1885). Dubar (1960, p. 52) has given the most detailed previous description of this taxon, and he also pointed out the differences between his specimens and the other species of *Otoites* which had been figured up to that time. The criteria separating *E. (O.) douvillei* from *E. (O.) fortis* (Westermann), with which it has been equated (Westermann 1954, p. 103), were given by Dubar (1960) as: its small size, being half to one-third of that of other *Otoitids*, the very strong contraction of its body chamber, and the modification of its ornament near the mouth border, particularly the loss of tubercles or nodes on the last two ribs. These characters appear perfectly valid, although there is some variation in the amount of contraction of the body chamber, since not all specimens show this to the same degree, notably those figured by Douville (1885, pl. III, fig. 9) and Lanquine (1929, pl. ix, fig. 6). It is also interesting to note Dubar's comment (*op. cit.*, p. 52) 'The exact age of this small form is still to be established . . . perhaps this *Otoites* will be the most ancient';

as it can now be shown that this species is indeed the oldest yet recorded belonging to the subgenus *Otoites*.

There are really no other species of *Otoites* closely related to *E. (O.) douvillei*, since they are all of much larger size and occur at higher stratigraphic horizons. In fact the most closely related forms are the more inflated variants of *T. (T.) cricki* nov. which are found together at the same horizon. These two groups are very much alike in size and relative proportions, the main difference being in the style of ribbing. It is thus reasonable to suggest that *E. (E.)/(E.) Otoites* evolved from the *T. (T.)/T. (Emileites)* group at the base of the *laeviuscula* Zone, especially since no specimens of either *Otoites* or *Emileia* have been found below this horizon.

Genus *Trilobiticeras* Buckman, 1919

Type species. Trilobiticeras (Trilobiticeras) trilobitoides Buckman, 1919 (m.).

Subgenus *Trilobiticeras* Buckman, 1919

Diagnosis. A group of very small-sized microconch ammonites, with coronate inner whorls. It has sharp primary ribs, which are terminated by sharp tubercles or spines at the point of division into the fine secondary ribs. The secondaries, of which there are three to five per primary, sweep forward over an arched venter. The body chamber shows an uncoiling of the umbilical seam, a coarsening of the tubercles and secondary ribs, a fading of the primary ribs, and it is terminated by a well-differentiated mouth border, with two spatulate lappets. The stratigraphic range of the subgenus is the same as that of *Emileites*, its macroconch counterpart, that is, upper *concaum* Zone to middle *laeviuscula* Zone.

Trilobiticeras (Trilobiticeras) cricki sp. nov.

Plate 17, figs. 1–3 and 5; text-fig. 2

1885 *Sphaeroceras sauzei* (variété ?); Douvillé non d'Orbigny, p. 41, pl. III, fig. 10.

1894 *Sphaeroceras* sp. nov.; Crick, p. 436.

1972 *Trilobiticeras trilobitoides* Buckman; Galacz non Buckman, pp. 43–44, text-fig. 2a–d.

1974 *Trilobiticeras* sp. nov.; Parsons, p. 169.

EXPLANATION OF PLATE 17

(All specimens are coated with ammonium chloride.)

Fig. 1a–b. *Trilobiticeras (Trilobiticeras) cricki* nov. (m.), holotype, BMNH. C79426, *in situ* bed 2, Barns Batch Spinney (Buckman and Wilson 1896), Dundry Hill, Bristol; $\times 1.5$.

Fig. 2a–b. *T. (T.) cricki* nov., first paratype, BMNH. C79427, *in situ* bed 2, Barns Batch Spinney; $\times 1.5$.

Fig. 3a–b. *T. (T.) cricki* nov., third paratype, BMNH. C75287, Dundry; $\times 1.5$.

Fig. 4. *Emileia (Otoites)* sp. cf. *E. (O.) douvillei* nov. (m.), Reed Collection, Yorkshire Museum, YM. 989, the 'fossil-bed', Sandford Lane, Dorset; $\times 1.0$.

Fig. 5. *T. (T.) cricki* nov., second paratype, BMNH. C79425, *in situ* bed 2, Barns Batch Spinney; $\times 1.5$.

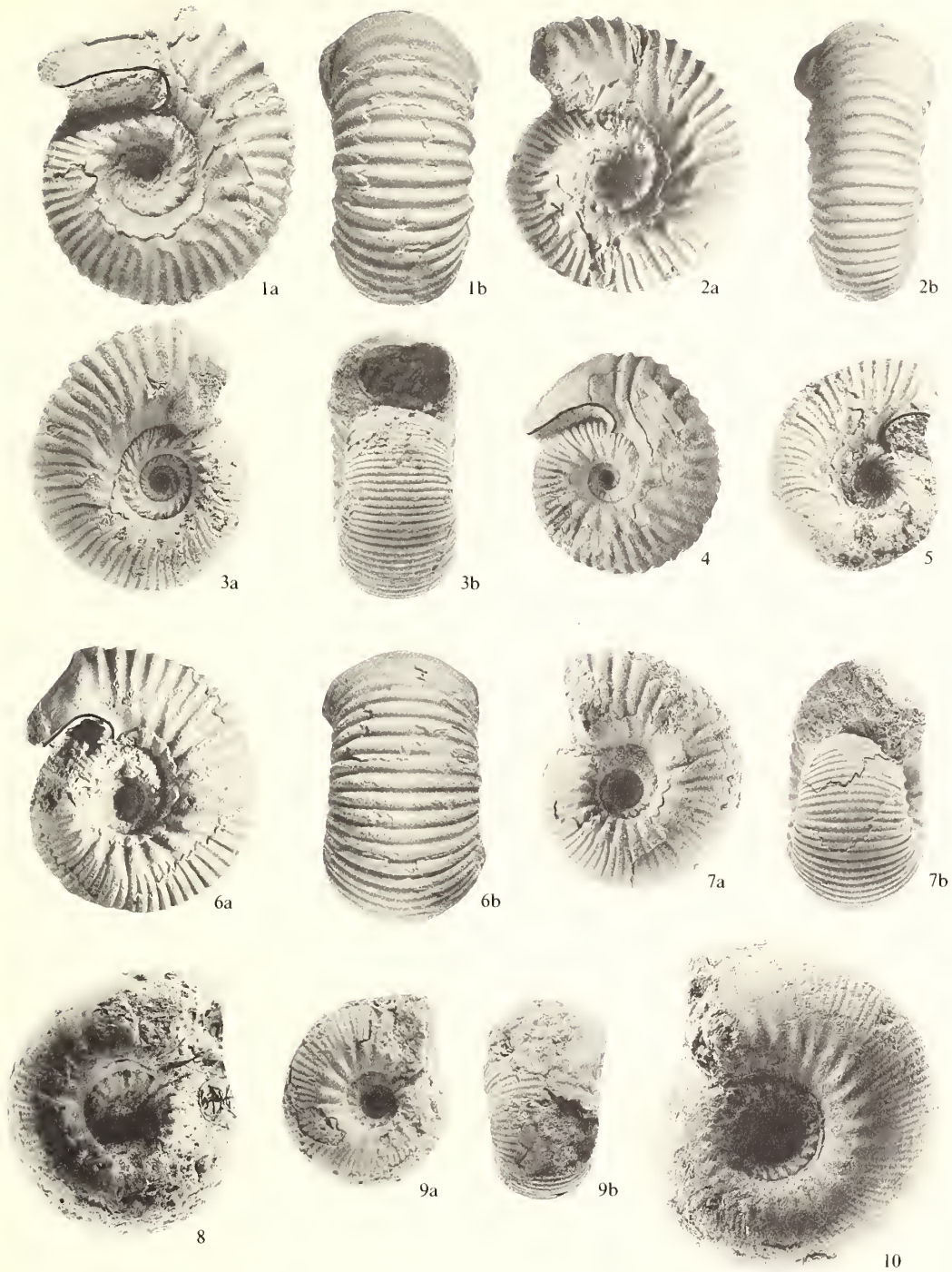
Fig. 6a–b. *E. (O.) douvillei* nov. (m.), holotype, Cb. 4744, Dundry; $\times 1.5$.

Fig. 7a–b. *E. (O.) douvillei* nov., fifth paratype, BMNH. C75242; $\times 1.5$.

Fig. 8. *E. (Emileia) subcadiconica* S. Buckman (M.), BMNH. C75279, Dundry; $\times 1.0$.

Fig. 9a–b. *E. (O.) douvillei* nov., first paratype, BMNH. C79429, *in situ* bed 2, Barns Batch Spinney; $\times 1.5$.

Fig. 10. *T. (Emileites) malenotatus* (S. Buckman) (M.), BMNH. C73979, Dundry; $\times 1.0$.



PARSONS, Bajocian otoitid ammonites

Material. Three specimens from the top 10 cm of bed 2, Barns Batch Spinney, Dundry Hill, Bristol, BMNH. C79425–79427; one specimen from bed 4b, Seavington-St.-Mary (ST 398 144), Somerset (Parsons and Torrens in Torrens 1969, p. A27), BMNH. C79433; one specimen from bed 6, Bruton Railway quarry, Bruton, Somerset, BMNH. C79431; one specimen from the base of the 'fossil-bed', Sandford Lane, Sherborne, Dorset (Buckman 1893, p. 492, bed 6), BMNH. C79430; one specimen from Cape Mondego, Portugal (Ruget-Perrot 1961, p. 27, bed 5), BMNH. C79435; one specimen from Bradford Abbas, near Sherborne, Dorset, SM. J24550; and three Dundry specimens from old museum collections, BMNH. C75270, C75287, and OUM. J1163. A total of eleven specimens, plus numerous (+100) other less well-localized specimens in various old museum collections.

Dimensions. Holotype, BMNH. C79426, a complete specimen, with lappets and three-quarters of a whorl of body chamber.

D	Ud	Pn	Wh	Wb	Wb Wh
2.82	0.96 (34%)	17	1.19 (42)	1.36 (48)	1.14
2.23	0.75 (34)	16	1.0 (45)	1.32 (59)	1.32

First paratype, BMNH. C79427, a complete specimen, with lappets and three-quarters of a whorl of body chamber.

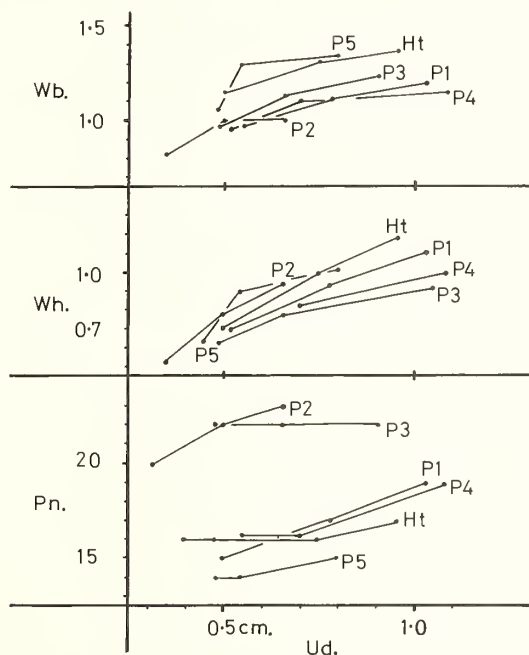
2.85	1.03 (36)	19	1.11 (39)	1.2 (42)	1.08
2.2	0.78 (36)	17	0.94 (43)	1.11 (51)	1.18

Second paratype, BMNH. C79425, a complete specimen, with lappets and three-quarters of a whorl of body chamber.

2.14	0.66 (31)	23	0.95 (44)	1.0 (47)	1.05
1.65	0.50 (30)	22	0.78 (47)	1.0 (61)	1.28

Description. A small microconch ammonite (maximum diameter, modal value from ninety-five specimens = 2.65 cm), with cadicone inner whorls and a rapid contraction of the body chamber, which extends for three-quarters of a whorl. The primary ribs are sharp, prorsiradiate, and approximately one-third of the length of the secondaries. The secondary ribs are extremely fine on the inner whorls, where there are three to five per primary, whilst on the outer whorls, where there are only two to three per primary, they are coarser and more widely spaced. The fine, sharp tubercles at the point of division of the secondary ribs, become stronger on the body chamber, whilst the primary ribs weaken, and in some cases become virtually obsolescent. The primary rib density is fairly constant on the inner whorls, but shows a marked increase on the penultimate and last whorls, see text-fig. 2. This rib density varies from individual to individual, between 14 and 23 ribs per whorl, the majority of specimens having in the region of 17 to 18 on the last whorl. The contraction of the body chamber results in a relative reduction in whorl breadth, as is clearly shown in text-fig. 2. Since the whorl height continues to increase, although at a reduced rate, right up to the mouth border, there is a pronounced change in the whorl cross-section; the cadicone inner whorls, with an arched venter ($Wb/Wh = 1.32$), take on a more rounded cross-section ($Wb/Wh = 1.14$). The mouth border is characterized by fine spatulate lappets, which develop in the mid-whorl position, see Plate 17, fig. 1a, and which are usually preceded by a more coarse and prominent secondary rib. Although the inner whorls are cadicone, the contraction of the body chamber gives a more planulate appearance to the mature shell, which is one of the more evolute ootitid microconchs ($Ud/D \times 100 = 30\text{--}40\%$). The suture line is difficult to make out on most specimens, but it appears similar to that of the Hungarian specimen (Galacz 1972, fig. 2).

Type series (the six well-localized specimens). The holotype (BMNH. C79426), is one of the dominant morphotypes (Pl. 17, fig. 1*a-b*), whilst the first paratype (BMNH. C79427) is a slightly less inflated and more finely ribbed variant (Pl. 17, fig. 2*a-b*). The second paratype (BMNH. C79425), is a small, even more finely ribbed form (Pl. 17, fig. 5). All three of the above specimens were collected *in situ* from bed 2 (top 10 cm), Barns Batch Spinney, Dundry Hill. The third paratype from Dundry (BMNH. C75287, *ex* Charlesworth Coll.), is a large fine ribbed specimen (Pl. 17, fig. 3*a-b*), whilst the fourth (BMNH. C75270, *ex* Pratt Coll.) is one of the more evolute forms. Finally the fifth paratype (OUM. J1163, *ex* Goddard Coll.), also from Dundry, is the most coarsely ribbed form I have seen; at a diameter of 2.4 cm, with more than two-thirds of a whorl of body chamber, it has fifteen primary ribs, at an umbilical diameter of 0.8 cm (33%).



TEXT-FIG. 2. A plot of whorl breadth (Wb), whorl height (Wh), and number of primary ribs (Pn), against umbilical diameter (Ud), for *Trilobiticerases cricki* sp. nov. Ht = holotype; P = paratype.

Sexual dimorphism. This group has well-marked sexual dimorphism and *Trilobiticerases* (*T.*) *cricki* nov. exhibits typical microconch features: small size, with well-developed lappets. The corresponding macroconch, although not quite as abundant as its partner, is well represented in the *ovalis* bed at Dundry. These specimens are identical in shell form, style of ribbing, and general ornament, to all but the last whorl of *T.* (*T.*) *cricki* nov., but differ by still being wholly septate at a diameter in

excess of that attained by mature specimens of the latter. A typical *ovalis* bed macroconch specimen from Dundry (BMNH. C73979) is figured here (Pl. 17, fig. 10). This has one whorl of body chamber at a diameter of 5.05 cm. There are two specific names available for this group. The type specimen of *T. (Emileites) malenotatus* (Buckman 1927, in 1909-1930, pl. 702, IGS. 49293), although rather fragmentary and poorly localized, is undoubtedly very similar to many of these macroconchs. As noted by Buckman (loc. cit.), the matrix of this specimen is typical of the *ovalis* bed of Dundry. The type specimens of *T. (E.) liebi* (Maubeuge 1955, pl. 9, figs. 1a-d and 2) are even closer in gross morphology to the Dundry forms, and it is likely that this species is a subjective junior synonym of *T. (E.) malenotatus*.

Stratigraphic range. The majority of members of this species have come from the *ovalis* bed of Dundry, which is *ovalis* Subzone, *laevinscula* Zone in age (Parsons 1974, p. 169). The lowest occurrence of this species appears to be the *discites* Zone. A single specimen from Bradford Abbas, near Sherborne, Dorset (SM. J24550), has the 'iron-shot', black-stained matrix typical of the top part of the Bradford Abbas 'fossil-bed', which is of this age (Parsons 1974, p. 170). A few specimens have been found as high as the *laevinscula* Subzone of the *laevinscula* Zone at Sandford Lane quarry, Sherborne (BMNH. C79430; Buckman 1893, p. 492, bed 6c) and at the South Main-road quarry (ST 567655), Dundry (CP. 2403; Buckman and Wilson 1896, p. 691, bed 5).

Geographic range. Outside of the localities in southern England mentioned above, this species has been figured from Hungary (Galacz 1972, fig. 2) and south-east France (Douvillé 1885, pl. III, fig. 10; M.121), whilst I have collected it from Cape Mondego, Portugal (BMNH. C79435; Ruget-Perrot 1961, p. 27, bed 5).

Discussion. This species is named in honour of G. C. Crick, who first noticed its presence in the Inferior Oolite of Dundry Hill (Crick 1894, p. 436). *T. (T.) cricki* nov. is closest in gross morphology to specimens from the upper *concauum*/lower *discites* Zones of southern England, which have been included in *T. (T.) punctum* (Vacek); (Westermann 1964, pl. 6, figs. 5-6). It is difficult to establish if the small, fragmentary type specimen of this latter species (ibid., pl. 6, fig. 7a-b) is truly conspecific with the larger specimens figured by Westermann (loc. cit.), from Seavington-St.-Mary, Somerset. If it is, then this group is consistently more inflated, with a more depressed and coronate whorl section than *T. (T.) cricki*. These two also have distinct stratigraphic distributions at Seavington-St.-Mary. The more inflated forms, *T. (T.) punctum*, are relatively common in bed 3 (Parsons and Torrens in Torrens 1969, p. A27), which is upper *concauum* Zone in age, whilst the specimen of *T. (T.) cricki* (BMNH. C79433), came from a higher horizon, bed 4b, which is *ovalis* subzone in age. However, the possibility must remain that the lectotype of *T. (T.) punctum* is nothing but the poorly preserved inner whorls of a specimen of *T. (T.) cricki*, rather than of the other congeneric, but stratigraphically lower, group. Unfortunately there is no definite solution to this problem, as the lectotype of *T. (T.) punctum* is virtually uninterpretable.

The only other species of *Trilobiticer*s, *T. (T.) trilobitoides* Buckman and *T. (T.) platygaster* Buckman, both have considerably more coronate inner whorls, a stronger

contraction of the body chamber, and more prominent spines and tubercles. The primary rib density of these two species is also consistently lower at fourteen to eighteen per whorl (average fifteen). As noticed by Crick (1894, p. 436), there is a considerable resemblance between some specimens of *T. (T.) cricki* and members of the *Pseudotoites* group, particularly *P. (Latotoites) evolutum* (Tornquist), (Westermann 1964, pl. 9, fig. 5). Whilst this resemblance could be nothing but another example of convergent evolution and homeomorphy, taking their relative stratigraphic positions into account, it is possible that these antipodean forms evolved from the *Trilobiticerat*/*Emileites* group at the base of the *laeviuscula* Zone.

PHYLOGENETIC SIGNIFICANCE OF NEW TAXA

One of the main requirements for establishing a phylogenetic relationship is a detailed stratigraphic knowledge of the groups concerned. There have been considerable problems in the past in the interpretation of the early history and evolution of the ammonite family Otoitidae. This has largely been due to the inadequate and often erroneous stratigraphic information available to fill the apparent gap between the first well-documented faunas of the *discites* Zone and the diverse and abundant forms of the *sauzei* Zone. One obvious source of confusion has been the error introduced by Mascke (1907) and perpetuated by Westermann (1954); that is, the artificial stratigraphic separation of the microconch *Otoites* above its macroconch counterpart *Emileia*. The other major stratigraphic error which has compounded the difficulties inherent in interpreting the early history of the Otoitids, has centred on the correlation of the horizons now included within the *laeviuscula* Zone. Buckman (1909–1930), when describing several new otoitid species from these horizons, referred them to more than six different hemerae (approximately equal to subzone in present use). When these hemerae were subsequently replaced by Oppel's reinstated *sowerbyi* Zone (Spath 1936), there was little or no evidence available on the correct stratigraphic age of Buckman's taxa. This is particularly true of the faunas ascribed to the 'so-called' *trigonalis* subzone, which were an artificial combination of species from at least two separate horizons (see Parsons 1974, pp. 162–164, 171, for further details). Because of this confusion it has in the past proved impossible to subdivide the highly diverse otoitid faunas found below the *sauzei* Zone (Arkell 1956, p. 33). This unfortunately led Westermann (1964, text-fig. 14) to use dominantly morphological rather than stratigraphic criteria to establish his otoitid phylogeny.

Recent work has revealed that there are numerous inconsistencies present in Westermann's phylogenetic scheme. Groups such as *Labyrinthoceras* and *Frogdenites*, which were linked as macroconch and microconch are now known to occupy different stratigraphic horizons in the *sauzei* and *laeviuscula* Zones respectively, whilst other groups, such as *E. crater*, *E. catamorpha*, *E. brocchii*, and *E. (Otoites) delicata*, which were separated by Westermann, are now known to occur together in the lower part of the 'fossil-bed', Sandford Lane, near Sherborne, Dorset (Parsons 1974, p. 168). It has now proved possible to determine the correct stratigraphic position of most members of the Otoitinae, an essential step prior to establishing

any phylogenetic relationships. The successive otoitid faunas from southern England (after Parsons 1974, pp. 164–171, with additions), are as follows:

(i) *concaum* Zone, rare specimens of *Trilobiticeras* (*T.*) '*punctum*', and its undescribed macroconch, *T. (Emileites)* sp. nov., both of which are morphologically very similar to the *Abbasites* group from the subjacent horizons.

(ii) *discites* Zone, rare specimens of *T. (T.) trilobitoides*, *T. (T.) platygaster* and two undescribed macroconchs, *T. (Emileites)* spp. nov., along with extremely rare specimens of *T. (T.) cricki* nov.

(iii) *ovalis* Subzone, relatively common specimens of *T. (T.) cricki* nov., *T. (E.) malenotatus*, *E. (E.) subcadiconica*, and *E. (Otoites) douvillei* nov.

(iv) *laeviuscula* Subzone (lower part), a diverse fauna of *E. (E.) brocchii*, *E. (E.) catamorphia* Buckman, *E. (E.) contrahens* Buckman, *E. (E.) crater* Buckman, *E. (E.) polyschides* (Waagen), *E. (Otoites) delicata* (Buckman), *E. (O.) douvillei* nov., *E. (O.) sauzei* (d'Orbigny) group, *T. (T.) cricki* nov., and *T. (Emileites)* sp.

(v) *laeviuscula* Subzone (upper part), *E. (E.) brocchii*, *E. (E.) bulligera* (Buckman), *E. (E.) polyschides*, *E. (Otoites) fortis* (Westermann), *E. (O.) sauzei* group, *Frogdenites extensum* (Buckman), *F. gibberulum* (Buckman), and *F. spiniger* Buckman.

(vi) *sauzei* Zone, *E. (E.) bulligera*, *E. (E.) greppini* Maubeuge, *E. (E.) multifida* Buckman, *E. (E.) polyschides*, *E. (E.) pseudocontrahens* Maubeuge, *E. (Otoites) sauzei* group, and *E. (O.) contracta* (Buckman non Sowerby).

In most of the above faunas, mainly due to lack of material, it is still difficult to specifically link micro- and macroconchs. Thus, except in the case of *Frogdenites*, where the dimorphism is manifestly intraspecific in character, in the bulk of the Otoitinae, following Callomon (1963), dimorphism is best expressed at the sub-generic level. Since morphological diversity is lower in the microconch groups, it is easier to establish a phylogenetic link between their successive populations. A summary of the stratigraphic distribution and probable phylogeny of the main microconch members of the Otoitinae is thus shown in text-fig. 3.

It is clear from this figure that the two new species are of critical phylogenetic importance. *E. (O.) douvillei* is the earliest member of its subgenus and its close relationship with *T. (T.) cricki* finally establishes the *Emileia/Otoites* group as an offshoot of *Trilobiticeras*. *T. (T.) cricki* is of fundamental importance, as it proves to be the root-stock for several important otoitid groups, as well as a long-ranging taxon useful for demonstrating the continuity between the faunas of the *discites* and *laeviuscula* Zones.

The genus *Frogdenites* closely resembles *T. (T.) cricki*, whilst its early members, such as *F. extensum*, also have an overlapping stratigraphic range: both *F. extensum* and *T. (T.) cricki* occur abundantly together in the middle *laeviuscula* Zone of Cape Mondego, Portugal (pers. obs.; Ruget-Perrot 1961, p. 27, bed 5). Specimens of *F. extensum* from north Dorset ('green-grained marl', Osborne Wood, Parsons 1974, p. 167), exhibit relatively coronate inner whorls, with a rapid uncoiling of the umbilical seam, in a similar fashion to *T. (T.) cricki*, to give a more planulate overall shell form. Only the relatively late forms, such as *F. spiniger*, have developed the

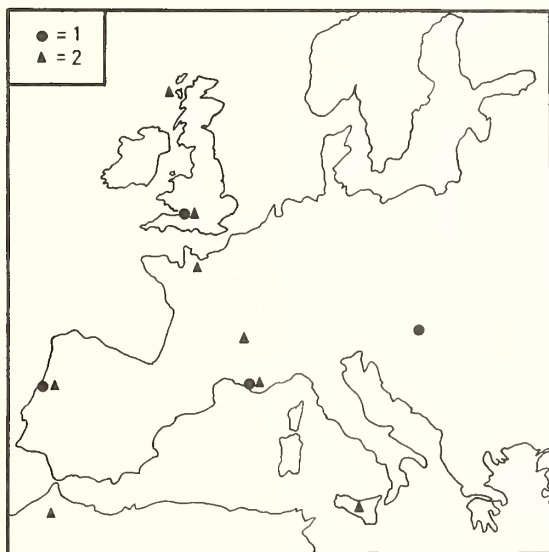
more inflated, involute, sphaeroconic form, which is transitional to the Sphaeroceratinae. *T. (T.) cricki* thus shows both a similar shell form, with coronate inner whorls and fine sharp tubercles, and a similar style of dimorphism, with a low size ratio between dimorphs, to that exhibited by *Frogdenites*. Since *T. (T.) cricki* is the only group to show these characters, which has a contiguous stratigraphic range with *Frogdenites*, it thus forms a highly probable ancestor for the latter genus.

The connection between the *Pseudotoites* group and *T. (T.) cricki* is the most tenuous of the three phylogenetic relationships suggested. *Pseudotoites*, particularly in Western Australia, is cryptogenic, as it appears suddenly in a geographically and stratigraphically isolated horizon, the Newmarracarra Limestone (Arkell and Playford 1954). The only way to determine the origins of such a group is to attempt to establish its relative stratigraphic position, and its similarities and affinities, if any, with possible related groups. The genus *Fontannesia* is abundant in Western Australia, where it forms a monospecific swarm at the base of the Newmarracarra Limestone (ibid., text-fig. 2). *Fontannesia* is found dominantly in the *discites* Zone in Europe, although it possibly ranges up into the base of the *laeviuscula* Zone (Pavia and Sturani 1968, p. 311). It is significant that this genus has been found in New Guinea associated with '*Docidoceras*' *longalvum* (Vacek), another *discites* Zone form (Westermann and Getty 1970). This would suggest that the succeeding *Pseudotoites* fauna (Arkell and Playford 1954, text-fig. 2), is just post-*discites* Zone in age. Since both *Fontannesia* and *Docidoceras* are predominantly Tethyan in origin (Arkell 1956, pp. 177 and 209; Westermann and Getty 1970, p. 291), it is logical to seek the ancestors of the *Pseudotoites* group in the Otoitids of the Tethyan *discites* Zone.

The *Pseudotoites* group shows a high degree of morphological diversity. The Australian macroconchs (*Pseudotoites* s. str.), are medium-sized, relatively inflated forms, with inner whorls exhibiting numerous, fine prorsiradiate secondary ribs (Arkell and Playford 1954, pl. 32, fig. 3), very similar to the *T. (E.) malenotatus* figured here (Pl. 17, fig. 10). The outer whorls show a modified ornament, with the development of short, inflated, nodate primary ribs. This is a similar trend to that shown by some undescribed specimens of *Emileia* from the lowest *laeviuscula* sub-zone at Dundry. The corresponding microconchs (*Pseudotoites* (*Latotoites*) spp.), included by Arkell in *Otoites* are similar to the latter genus in ribbing style, but differ by being much more evolute. They are thus similar in many characters, except size, to *T. (T.) cricki* nov. There are rare specimens in the Australian faunas which show a close similarity with members of the *T. (T.) trilobitoides* Buckman group: *P. (Latotoites) depressus* (Whitehouse), (Arkell and Playford 1954, pl. 30, fig. 7). Arkell was hesitant about including the latter taxon in *Trilobiticerias* because of its greater size (c. 4.0 cm), compared to the much smaller European *Trilobiticerias* known at that time. The description of *T. (T.) cricki*, with a maximum diameter in excess of 3.1 cm has thus removed one serious objection to any comparisons between these groups.

On both general morphological and stratigraphic grounds, there is thus no really plausible existing alternative to accepting the *Trilobiticerias*/*T. (Emileites)* group as the root stock of *Pseudotoites*. If *Pseudotoites* did not evolve directly from the *T. (T.) cricki* group, then they both must have had a common ancestor in the *discites* Zone. An interesting problem is presented by the relationship of the above groups to the genus *Docidoceras*. As pointed out by Arkell (Arkell and Playford 1954, p. 572), the

type species of this genus, *D. cylindroides* S. Buckman, bears a close morphological relationship to some members of the *Pseudotoites* group. The former species is in fact atypical of the rest of the forms included in *Docidoceras* by Buckman (1909–1930) (Arkell and Playford 1954, p. 572). There is thus a possibility that this species may have had a common origin, with *Trilobiticeras*/*Emileites*, in the *concauum* Zone *Abbasites*, a suggestion already made by Westermann (1969, pp. 129 and 137). The bulk of the other 'species' of '*Docidoceras*', with their more typically stephanoceratid ribbing style, are undoubtedly closely related to some as yet undescribed species, akin to '*D. longalvum*' (Vacek), from the middle *murchisonae* Zone of south Dorset (Senior *et al.* 1970—*Docidoceras* sp., Horn Park quarry, bed 5a). The genus *Docidoceras*, as at present defined, could thus be polyphyletic. It seems certain that *Docidoceras*, taking into account its stratigraphic range and gross morphology, makes a poor dimorphic partner for *Trilobiticeras*; on these grounds *Emileites* is far more satisfactory.



TEXT-FIG. 4. The geographic distribution of 1, *Trilobiticeras* (*Trilobiticeras*) *cricki* sp. nov., and 2, *Emileia* (*Otoites*) *douvillei* sp. nov.

STRATIGRAPHIC SIGNIFICANCE

The two species described here jointly have a restricted stratigraphic range (text-fig. 3) and a wide geographic distribution (text-fig. 4). They thus form an important part of an ammonite fauna, which over most of Europe is characteristic of the basal *ovalis* subzone of the *laeviuscula* Zone (Parsons 1974). Whilst the constituent members of this fauna remain much the same, their relative proportions vary according to geographic position. In southern England, a fairly typical fauna from Barns Batch Spinney, Dundry, has the following proportions: *Witchellia* 46 specimens, *Sonninia* 10, *Trilobiticeras* 17, *Emileia* 2, *Docidoceras* 1, *Bradfordia* 6, *Strigoceras* 2.

To the north in Skye (Inner Hebrides, Scotland), the Sonninidae are almost totally dominant, as apart from an isolated specimen of *E. (O.)* cf. *douvillei* nov., only specimens of *Sominia s. lat.* and *Witchellia* have been recorded (pers. obs.; Morton 1975). South towards Tethys the Sonninidae become progressively less abundant as there is an increase in diversity linked with a levelling out of the relative proportions of the different ammonite groups present. On the whole in Tethyan and adjoining regions, the Stephanoceratacea and Haploceratacea are the more important. Of these, the genus *Bradfordia* is particularly characteristic of the Lower Bajocian in Bulgaria (Sapunov 1971), Sicily (Renz 1925), and Portugal (pers. obs.). The major exception to this trend appears to be south Germany, where probably due to palaeogeographic isolation, the faunas are largely restricted to *Sominia s. str.* The most important areas of preservation of *ovalis* subzone faunas in Europe are to be found in England, France, and Germany.

Southern England

The best exposures of rocks assigned to this subzone in England are to be found on Dundry Hill, near Bristol. Here sections at Castle Farm (Buckman and Wilson 1896, p. 676), Barns Batch Spinney (ibid., p. 689), South Main-road (ibid., p. 691), and Rackledown (ibid., p. 692), have all yielded abundant *ovalis* subzone faunas. The most extensive collection from this horizon (the 'Lower white iron-shot'), has been made at Barns Batch Spinney (ibid., p. 689, bed 2), and this includes: *Witchellia (Witchellia) albida* (S. Buckman); *W. (W.) romanoidea* (Douvill ); *W. (W.)* cf. *connata* (S. Buckman); *W. (W.)* cf. *sutneri* (Branco); *W. (Pelekodites) pelekus* (S. Buckman); *W. (P.)* cf. *macra* (S. Buckman); *Sominia ovalis* (S. Buckman ex Quenstedt); *Euhoplloceras* sp.; *Bradfordia* cf. *inclusa* S. Buckman; *Strigoceras compressum* (S. Buckman); *Toxamblytes* sp.; *Docidoceras* cf. *cylindroides* S. Buckman; *Trilobiticeras (T.) cricki* nov.; *T. (Emileites) malenotatus* (S. Buckman)-*T. (E.) liebi* (Maubeuge) group; *Emileia (Otoites) douvillei* nov.

Other areas in England which have produced similar faunas include the Cotswold Hills (Buckman 1895, p. 397, beds 4-5); the Cole 'syncline', Bruton, Somerset (Richardson 1916, p. 495, bed 6); the Sherborne district, Dorset (Buckman 1893, p. 493, bed 8), and Seavington-St.-Mary, Somerset (Parsons and Torrens in Torrens 1969, p. A27, bed 4b).

France

The so-called '*Witchellia*-beds' of Normandy have produced a fauna of at least the *ovalis* subzone (Haug 1893; Bigot 1900; Gabilly and Rioult 1974). The most famous exposures of rocks of this age are, however, to be found to the south near Toulon (Douvill  1885). Here a thin, condensed limestone has produced one of the most diverse faunas from this subzone, which has been described in detail (ibid.). Whilst the stratigraphy and distribution of this bed is well known (ibid.; Lanquine 1929), the interpretation of its fauna has been difficult, as only a few specimens have been figured by modern methods (Lanquine 1929, pls. IX and X). For the rest only the rather stylized drawings provided by Douvill  (1885, pls. I-III) have been available. However, Douvill 's specimens are still preserved in the  cole des Mines Collections, now held at the Universit  de Paris-Sud. The latter has kindly provided

me with photographs of this material, which have enabled a more accurate interpretation of Douvillé's figures to be made:

Plate I, figure 1, *Euhoploceras* sp. 2, ?*E.* sp. 3 and 3a, *E.* sp. 4, *E.* cf. *palniata* S. Buckman. 5, *Witchellia* (*Pelekodites*) cf. *zurcheri* (Douvillé). 6, *W.* (*P.*) *zurcheri*, lectotype, designated by Buckman (1909–1930, pl. 399). 7, *W.* (*P.*) *zurcheri*. 8, *Zurcheria ubaldi* Douvillé.

Plate II, figure 1, *Witchellia* (*Witchellia*) *sayni* Haug. 2–5, *W.* (*W.*) spp.

Plate III, figures 1–2, *W.* (*W.*) sp. 3 and 3a, *W.* (*W.*) *romanoides* (Douvillé). 4, *W.* (*W.*) *romanoides*. 5, *W.* (*W.*) *romanoides*. 6 and 6a, *Bradfordia praeradiata* (Douvillé), lectotype, designated by Sapunov (1971, p. 79). 7, *Bradfordia* cf. *praeradiata*. 8, *Emileia* (*Emileia*) aff. *subcadiconica* S. Buckman. 9, *E.* (*Otoites*) *douvillei* nov. 10, *Trilobiticeras* (*Trilobiticeras*) *cricki* nov.

The two other specimens, which have been figured from this horizon by Lanquine (1929), are *Emileia* (*Otoites*) cf. *douvillei* nov. (ibid., pl. IX, fig. 6) and *Trilobiticeras* (*Emileites*) sp. (ibid., pl. X, fig. 2). This fauna, apart from its slightly higher apparent diversity, is identical to that recorded from Dundry Hill, England; the close similarity of the *Witchellia* groups is particularly striking.

Germany and Switzerland

The Schwabian Albe of south-west Germany and the adjoining Swiss Jura both possess fossiliferous representatives of the *ovalis* Subzone. The 'Unterer Wedelsandstein' of Schwabia (Parsons 1974, p. 173) is the source of the type specimen of *Somminia ovalis* (Buckman ex Quenstedt), and this species is by far the most abundant in these beds. Other less-common forms include rare specimens of *Witchellia* spp. and a solitary specimen of *T. (E.) liebi* (Maubeuge) (Bayer 1968; Parsons 1974, p. 175). The equivalent beds in the Swiss Jura have apparently yielded the type specimens of *T. (E.) liebi* (Maubeuge 1955, pl. 9, figs. 1a–d and 2), but this needs to be confirmed by the collection of *in situ* topotypes.

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SOME PHACOPINA (TRILOBITA) FROM THE SILURIAN OF SCOTLAND

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ABSTRACT. *Acernaspis* (*Eskaspis*), a new subgenus, and *Podowrinella*, a new genus of Phacopina from Silurian inliers of the Midland Valley of Scotland, are here proposed. *A. (Eskaspis)* is restricted to the Telychian (upper Llandovery) and is referred to the subfamily Phacopinae. *A. (E.) sufferta* (Lamont) from the *M. crenulata* Zone of the Pentland Hills and *A. (E.) woodburnensis* from the upper *M. sedgwickii* Zone of Girvan are described. *Podowrinella*, which is found in the lower Wenlock of Girvan, and in the Telychian (upper Llandovery) of the Hagshaw and Pentland Hills, can probably be assigned to the Pterygometopidae, but possesses some character states normally considered representative of Phacopidae. Coaptative structures on the ventral doublures of *A. (Eskaspis)* and *Podowrinella* are described in detail, and information is given on the auxiliary impression system on the glabella of *A. (E.) sufferta*.

SILURIAN rocks in the Midland Valley of Scotland lie in a chain of inliers extending from Girvan to within a few kilometres of Edinburgh (text-fig. 1). At Girvan, in the Hagshaw Hills, and in the North Esk Inlier of the Pentland Hills, the Llandovery succession begins with turbidites or subturbidites, and passing upwards through shallow-water marine horizons (with shelly faunas well developed at certain horizons at Girvan and in the North Esk Inlier) the sequence changes to thin brackish or freshwater deposits and finally into redbeds, early in the Wenlock.

The large inlier of Lesmahagow, lying further to the north, has dominantly fresh or brackish water beds followed by redbeds.

In Telychian (upper Llandovery) mudstones and siltstones of the North Esk Inlier there occur abundant faunas, especially in the beds which have been referred to as the '*Plectodonta* mudstones' by Lamont (1947) and others.

Fossils were first discovered here in 1838 by Charles Maclaren of the Geological Survey, and Howell and Geikie listed them in 1861. The fine preservation and richness of the faunas led to much palaeontological activity in the next few decades, mainly by members of the Edinburgh Geological Society and associates (Haswell 1865; Henderson 1867; Brown and Henderson 1867; Henderson and Brown 1869; Etheridge 1874; Davidson 1874). But although extensive faunal lists were compiled, only Haswell (1865) and Davidson (1874) described any of the faunal elements. Haswell's descriptions and plates were very sketchy, but Davidson's monograph of the brachiopods was a valuable and enduring contribution to the palaeontology of the region.

The U.K. Geological Survey's faunal notes were updated by Peach and Horne (1899) and Mykura and Smith (1962), who described the area in detail.

Meanwhile, Lamont (1947, 1948, 1949, 1952) discussed the fauna at length primarily in a stratigraphical context, recognizing for the first time that the faunas were pre-Wenlock. New bivalves and chelicerates were later described (Lamont 1954, 1955). Though the starfish from well-known horizons in the Gutterford Burn were formally described by Spencer (1914–1940), most of the other elements in the

rich and diverse fauna of the Pentland Hills remained imperfectly known or undescribed until very recently. Interest in the fauna has revived of late, however, and various elements have been revised or described for the first time by various authors. In recent works there have been described a new echinoid (Kier 1973), crinoids (Brower 1975), and the trilobite *Scotoharpes* (Norford 1973).

Tipper (1976) has remapped the region, revised the stratigraphy, erected new formation names, and distinguished three successive faunal assemblages from the upper Deerhope and lower Wether Law Linn Formation (Tipper 1975). In the present paper Tipper's formation names have been used throughout, replacing the older stratigraphical divisions (text-fig. 1).

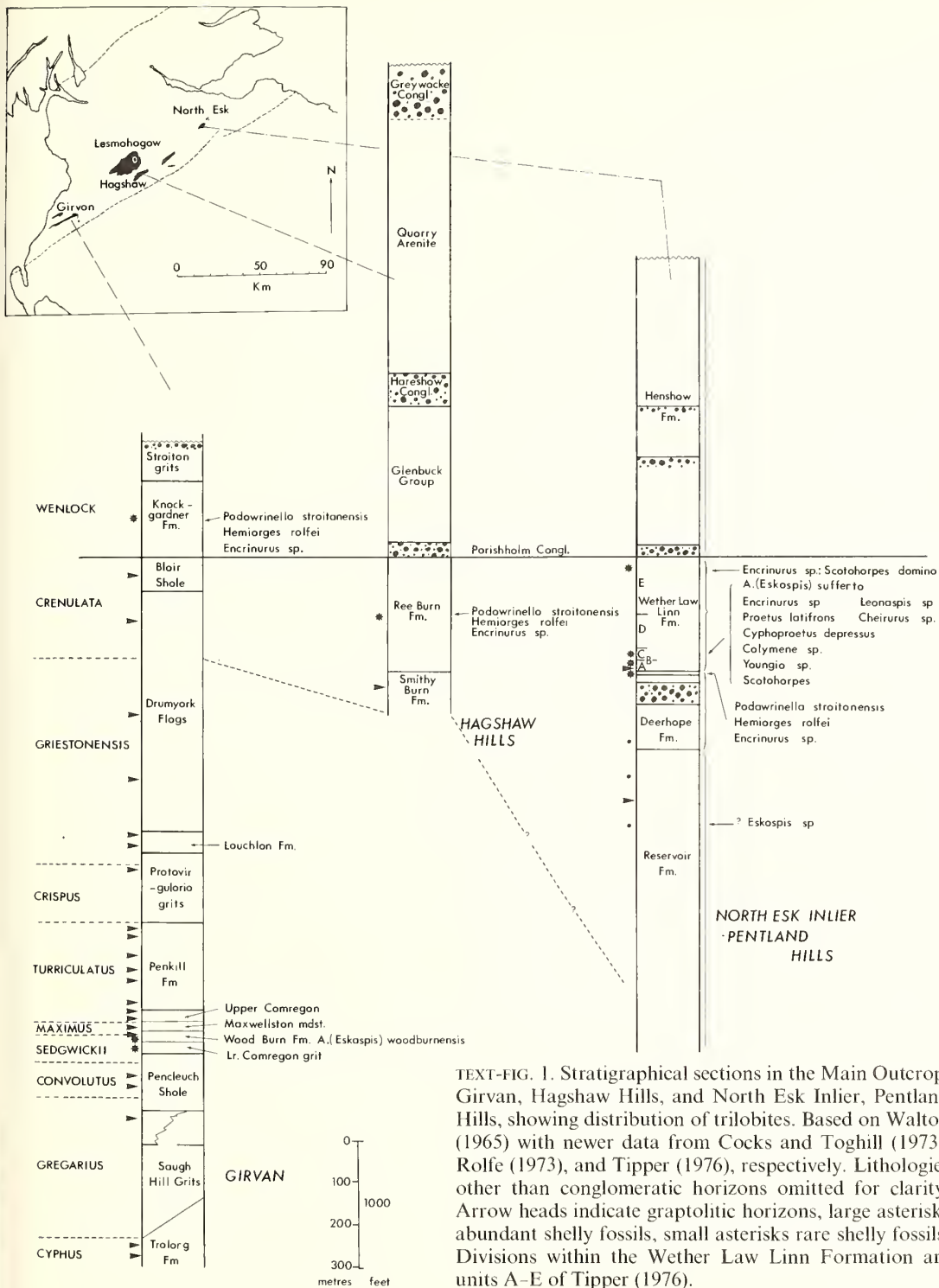
Trilobites, amongst many other fossils, especially brachiopods, are abundant at certain horizons within the upper Llandoverly, and though the fauna is restricted to a comparatively few genera and species, individuals of these may be frequently encountered. In the Reservoir Formation these include occasional phacopids, probably *Acernaspis* (*Eskaspis*), n. sg. otarionids and odontopleurids, whereas *Podowrinella straitonensis*, *Encrinurus*, and *Hemiarges* together with less-common elements are present at the top of the Deerhope Formation. In the immediately overlying Wether Law Linn Formation (which includes the *Plectodonta* Mudstones), there is a rich fauna with *A. (E.) sufferta* (Lamont) (150 examples), *Encrinurus* sp. (c. 150 ex.), *Proetus latifrons* (M'Coy) (25 ex.), *Cyphoproetus depressus* (Barrande) (16 ex.), *Scotoharpes domina* (Lamont) (2 ex.), *Youngia* (6 ex.), *Calymene* sp. (6 ex.), *Cheirurus* sp. (1 ex.), and possibly other genera and species listed by Lamont (1948), though the validity of these has not yet been ascertained.

In the Wether Law Linn Formation the most abundant trilobites are found only at the base (in units A and C of Tipper) becoming less common towards the top of unit C of the succession. *Encrinurus* occurs quite abundantly, however, in the uppermost part of this formation, in unit E, in which the only other trilobite to have been collected is *Scotoharpes*. Tipper (1975) has shown that trilobites occur independently of the brachiopod communities which he described in this sequence.

In this paper the Phacopina of the Pentland Hills are described, these being *A. (E.) sufferta* (Lamont, 1947) and *Podowrinella straitonensis* (Lamont, 1965). *A. (E.) sufferta* is known from the Pentland Hills alone, but an earlier species, *A. (E.) woodburnensis*, n. sp. from the older Wood Burn Formation at Girvan can also be referred to that genus, and is the only other species known at present.

P. straitonensis is known from the Ree Burn Formation in the Hagshaw Hills, from which it was first described from specimens collected by Rolfe, and also from the lower Wenlock Knockgardner Formation at Girvan. In the Pentland Hills it occurs in a coarse siltstone, whereas both in the Hagshaw Hills and at Knockgardner, specimens are found at the base of coarse turbidite flows where they occur with brachiopod faunas (Rolfe 1973; Cocks and Toghil 1973). In all these cases *Encrinurus* and *Hemiarges* occur in the same fauna, which, judging by its anomalous stratigraphic position (younger in the west), strongly indicates either a facies fauna (perhaps controlled in some way by the regressive sequence), or else inaccuracies in correlation.

The present work is the first of a series of papers in which the trilobite fauna of the Pentland Hills is described. The rest of the fauna will be described in later papers, some by other authors.



TEXT-FIG. 1. Stratigraphical sections in the Main Outcrop, Girvan, Hagshaw Hills, and North Esk Inlier, Pentland Hills, showing distribution of trilobites. Based on Walton (1965) with newer data from Cocks and Toghill (1973), Rolfe (1973), and Tipper (1976), respectively. Lithologies other than conglomeratic horizons omitted for clarity. Arrow heads indicate graptolitic horizons, large asterisks abundant shelly fossils, small asterisks rare shelly fossils. Divisions within the Wether Law Linn Formation are units A-E of Tipper (1976).

TAXONOMY

Nomenclature

Lamont (1965) described *Phacops straitonensis* from the Hagshaw Hills and Knockgardner. The discovery of this species in the Pentland Hills, and the collection of more material from all three localities gave the incentive for a more detailed study. No question arises over the validity of the specific name, though the holotype has been lost (Lamont, pers. comm.).

Podowrinella is here described as a new genus. It seemed to us initially that the poorly known, but suggestively named, genus *Pterygometopidella* Wedekind, 1912 (based on *Phacops quadrilineata* Angelin) might be available as a generic taxon for *P. straitonensis*. Wedekind (1912) described *Pterygometopidella* very inadequately from only two specimens collected from the c-marl (Silurian) of Gotland, and figured only one of them in a poor and tiny photograph which allowed few details to be seen but which seemed to indicate a close resemblance to *Eophacops musheni* (Salter). The two specimens, deposited in the collections of the Geologisch-Paläontologisches Institut der Universität Göttingen, are no longer in the Institute (Jahnke, pers. comm. 1974), and may have been destroyed. Struve (pers. comm. 1974) suggests that Wedekind may have erected the subgenus on an erroneously determined species and Schrank (1972) regards Wedekind's specimens of *P. quadrilineata* as incorrectly determined individuals of *E. musheni* (Salter), indicating that *Eophacops* is a junior synonym of *Pterygometopidella*.

Though the taxonomic problem of *Pterygometopidella* may not be entirely resolved, it is clear that this generic name is not available for *Phacops straitonensis*.

A. (E.) sufferta, on the other hand, was figured, though not described, by Lamont (1948) as *Eophacops sufferta*, in a paper in which many other trilobites from the Pentland Hills were also figured but for which no formal descriptions were given. There thus arises the question of the validity of the nomenclature, a matter which Norford (1973) has also referred to in dealing with *Scotoharpes*. *S. domina* Lamont was also figured in the same paper by Lamont (1948), and Whittington (1950) rejected the name as being invalid. Norford (p. 12), however, revived the name on the basis of Lamont's recognizable photograph and few words of description.

For the same reasons the specific name *sufferta* is here considered to be valid, since the photographs of Lamont's (1948, pl. 1, figs. 21, 22) which show a complete internal mould are clearly recognizable, and Lamont (pers. comm. 1974) has confirmed that the common phacopid trilobite at Wether Law Linn is, in fact his '*Eophacops*' *sufferta*, though the type, formerly in his possession, has now been lost. Though Lamont did not name the species in his 1947 paper on the stratigraphy and faunas of the region he states (p. 290) that 'a large *Eophacops* is very common at Wetherlaw Linn. It has more than 6 facets per radius in the eye, which rules out *E. elliptifrons* (Esmark). . . . The rather long pygidium with numerous axial segments, however, points to comparison with *E. elliptifrons* var *glaber* Marr & Nicholson . . .'. Lamont's notes which annotate the Grant Institute Library copy of Haswell's (1865) guide to the geology and faunas of the Pentland Hills refer to Haswell's figures (p. 6) of '*Phacops stokesii*' as '*E. sufferta*' and state, 'It should have shown 7-8 rings in the pygidial axis' and, 'Eye usually has 7 facets per column'.

There thus seems to be no question that the common and only species of phacopid trilobite from the Wether Law Linn Formation is what Lamont recognized as a new species and called *E. sufferta*, and it is here redescribed, under the generic name *Acernaspis* (*Eskaspis*).

SYSTEMATIC DESCRIPTIONS

Order PHACOPIDA Salter, 1864

Suborder PHACOPINA Struve, 1959

Superfamily PHACOPACEA Hawle and Corda, 1847

Family PHACOPIDAE Hawle and Corda, 1847

Subfamily PHACOPINAE Hawle and Corda, 1847

Genus ACERNASPIS Campbell, 1967

Subgenus ESKASPIS n. sg.

Type species. *Eophacops sufferta* Lamont, 1947. Upper Llandoverly (Telychian). Wether Law Linn Formation, North Esk Inlier, Pentland Hills, Peeblesshire, Scotland.

Diagnosis. Relatively small Phacopinae. Cephalon roughly 1.8 times as wide as long; genae somewhat truncate postero-distally (in dorsal view) so that the cephalon is widest just anterior to the posterior branch of the facial suture. Anterior glabella lobe moderately inflated, rather flat on top and shelving more steeply anteriorly.

Axial furrows deeply emplaced. Glabellar furrows 3p and 2p lightly impressed; 3p in two distinct, unjoined parts with distal ramus straight, running at an exsagittal angle of 45°, not confluent with axial furrow; proximal ramus of 3p furrows convex anteriorly, inclined slightly antero-laterally. 2p furrows likewise convex and not confluent with axial furrows.

Glabellar furrows 1p confluent with axial furrow, concave anteriorly and not coalesced mesially, with stout apodemes developed in distal portion of 1p external surface. Intercalating ring thus confluent mesially with anterior glabellar lobe; intercalating ring depressed, with distal nodes. Occipital furrow deeply incised laterally. Occipital ring longest (sag.) at the midline, depressed laterally with nodes partially set off by exsag. furrows, not reaching height of anterior glabellar lobe in lateral view.

Posterior border furrow lightly impressed, becoming nearly obsolescent laterally but merging with lateral border furrow. Eyes large, nearly reaching, or some distance from, posterior border furrow, and, anteriorly, lateral border furrow, with eye socle developed only as small, depressed area beneath visual surface. Visual surface with sixteen to nineteen dorsoventral files of lenses, all protruding well beyond bounding sclera. Palpebral lobe flat, rather narrow, set off from palpebral area by faint palpebral furrow.

Anterior cephalic margin distinct laterally and smoothly continuous with anterior glabellar lobe, disappearing antero-medially. No anterior border furrow developed.

Anterior doublure fairly long (sag.), with inflated central lobe sometimes present. Vicular furrow present anteriorly only as paired subfrontal depressions meeting at midline, deeply impressed postero-laterally and bearing nine notches for pleural

tips. Anterior and posterior regions of vincular furrow unconnected, or connected by a faint furrow. Hypostoma unknown.

All parts of exoskeleton minutely granular; auxiliary impression system ovate, developed as depressions devoid of granules on anterior glabellar lobe, and as scars viscerally.

Thorax with distinct axial nodes set off by short non-communicating furrows inclined postero-proximally on both the anterior and posterior sides of axial ring. Pleural tips gently rounded. Pygidium with well-defined axial furrows, with about six axial rings and terminal piece. Axis rounded posteriorly, not meeting posterior margin of pygidium. Five pairs of pleurae present; pleural furrows becoming progressively fainter posteriorly; inter-pleural furrows present, but weakly impressed.

Remarks. Our diagnosis of *Acernaspis* (*Eskaspis*) includes character states inclusive of some other, particularly Silurian, Phacopinae. All characters included in the diagnosis do, in fact, vary in general amongst Phacopinae and are of potential value as diagnostic elements. Furthermore, inclusion of 'primitive' as opposed to strictly autapomorphous ('derived') characters, in a diagnosis, is of value in recognizing distinct genera, for only one or at most a few subordinate taxa in a defined group may in fact retain a particular primitive feature, hence its valid inclusion in a diagnosis. The minute granulation of *A. (Eskaspis)*, for instance, is close to the primitive condition for all Phacopinae, yet is typical only of species of *A. (Eskaspis)* and *A. (Acernaspis)* among all known Phacopinae.

As written, the diagnosis of *A. (Eskaspis)* embraces some features of only three additional genera known to us: *Murphycops* Lespérance, *A. (Acernaspis)* Campbell, and in ventral morphology *Ananaspis* Campbell. We emphasize here the distinctly diagnostic traits of *Acernaspis* (*Eskaspis*) which serve to distinguish it from these other genera. *A. (Eskaspis)* shares with *Murphycops* some similarity in the coaptative device of the cephalic doublure, but otherwise differs from *Murphycops* in the cuticular granulation, development of auxiliary impression system, presence of a distinct palpebral furrow separating the palpebral lobe from the palpebral area, and the presence of nodes developed on the thoracic axial rings just proximal to the axial furrows.

A. (Acernaspis) and *A. (Eskaspis)* are dorsally very similar to one another, their over-all shape, degree of glabellar inflation, and auxiliary glabellar impressions, for instance are almost identical, and perhaps the only significant difference is the reduction of the anterior border in *A. (Eskaspis)*, so that it is not visible in dorsal view. But we would here draw attention to the ventral morphology of the cephalon, as did Campbell (1967), and because of the coaptative enrolment mechanisms, to the pygidial doublure. Coaptative morphology has not yet been fully explored in Phacopina, but is clearly very important in taxonomy.

The ventral cephalic morphology of *A. (Acernaspis)*, here represented by the Idwian *A. (A.) elliptifrons* (Esmark) from Girvan, Ayrshire, Scotland, is substantially different from that of *A. (Eskaspis) sufferata*. There are some variations within *A. (Acernaspis)* judging by the photographs of the doublures of various species given by Campbell (1967), Männil (1970a, b), and Sherwin (1972), but nowhere is there the

kind of conformation illustrated by *A. (E.) sufferta*. Both *elliptifrons* and *sufferta* have nine vincular notches, the last one being indistinct in *elliptifrons* (text-fig. 3a-c). In *elliptifrons* the vincular notches are narrow and all about the same width forming a more or less parallel-sided row deeply indenting the flat surface of the doublure and subparallel with its edges. The notches are all centrally excavated to about the same depth and are joined by shallower passages. The anterior notch runs into a deep vincular furrow behind which the doublure forms a pronounced flat shelf. *Sufferta*, on the other hand, has a much wider series of obliquely set vincular notches, becoming broader and deeper posteriorly and evidently adapted for receiving a flattened pleural end rather than a more pointed tip. The two ridges separated by the vincular notches are oblique to one another when seen in lateral view, and the outer one is indented by continuations of vincular notches. *A. (E.) sufferta*, the type species, has no trace of a vincular furrow, but has a pair of shallow subfrontal depressions meeting on the midline. *A. (E.) woodburnensis* has these subfrontal depressions as well, but also has a shallow vincular furrow joining each of them to the vincular notches. It is not a deeply incised furrow like that of *elliptifrons*, however, but a lightly impressed indentation. The vincular morphology of *woodburnensis* is in many ways intermediate between that of *elliptifrons* and that of *sufferta*, being anteriorly more similar to the former, and posteriorly resembling the latter; the three are illustrated here as a morphological series (text-fig. 3). In many ways, however, there is a fair resemblance between the vincular morphology of *woodburnensis*, to that of *Ananaspis* species (Campbell 1967, pl. 14, figs. 9, 13-15), though the presence of the subfrontal depressions links it with *Acernaspis (Eskaspis)* to which it is, with slight reservations, assigned here.

A. (Eskaspis) seems to have been a localized late Llandovery derivative of the *A. (Acernaspis)* stock, retaining most of its plesiomorphic (primitive) features of dorsal cephalic morphology, but having more advanced ventral morphology. This in *woodburnensis* is rather like that of the 'derived' genus *Ananaspis*, which it does not closely resemble in dorsal morphology, though it also has features pointing towards the more extreme, and indeed unique construction of the doublure of *Acernaspis (E.) sufferta*, which seems to have been a terminal endpoint.

Acernaspis (Eskaspis) sufferta (Lamont, 1947)

Plate 18, figs. 1-9; Plate 19, figs. 1-7, 10; text-figs. 2a, f, 3a, b, 4a, c

- 1861 *Phacops Stokesii* M.-Edw.; Howell and Geikie, p. 134.
- 1865 *Phacops Stokesii* Haswell, p. 37, pl. 4, figs. 6, 7.
- 1867 *Phacops Stokesii* Henderson, pp. 22-23.
- 1869 *Phacops Stokesii* Brown and Henderson, p. 31.
- 1899 *Phacops Stokesii* (M.-Edw.); Peach and Horne, p. 597.
- 1947a *Eophacops* cf. *elliptifrons* var. *glaber*. Marr and Nicholson; Lamont, p. 290.
- 1947b *Eophacops sufferta* n. sp. Lamont, p. 6, pl. 1, figs. 21, 22.
- 1962 *Phacops* aff. *stokesii* (Milne-Edwards); Mykura and Smith, p. 138.
- 1975 *Acernaspis* sp. Tipper, p. 297.

Material. Neotype, IGS 1034. Pl. 18, fig. 1, is here selected since Lamont's holotype is lost.

Other figured material. Gr. I. 40282, Pl. 18, fig. 2; Gr. I. 40279, Pl. 18, figs. 3, 7; IGS 5783, Pl. 18, fig. 4; Gr. I. 40269, Pl. 18, fig. 5; Gr. I. 40270, Pl. 18, fig. 6; Gr. I. 40262, Pl. 18, fig. 8; Gr. I. 40281, Pl. 18, fig. 9;

Gr. I. 40257, Pl. 19, fig. 1; Gr. I. 40243, Pl. 19, fig. 2; Gr. I. 40281, Pl. 19, fig. 3; Gr. I. 40260, Pl. 19, fig. 4; Gr. I. 40280, Pl. 19, fig. 5; Gr. I. 44093, Pl. 19, fig. 6; Gr. I. 40261, Pl. 19, fig. 7; Gr. I. 40275, Pl. 19, fig. 8; Gr. I. 44094, Pl. 19, fig. 10.

Additional material examined. Approximately 150 specimens from the Wether Law Linn Formation (Tipper's units A and C) from the Deerhope Burn and Wether Law Linn localities from the collections of the Grant Institute (Gr. I.) (mainly Tipper and Clarkson Collections), the Royal Scottish Museum (RSM), and the Institute of Geological Sciences (IGS) of Edinburgh.

Distribution. This species is confined to the lower Wether Law Linn Formation in the North Esk Inlier, Pentland Hills. It occurs quite abundantly and in good preservation as internal and external moulds at all levels, and complete specimens are not infrequently found. Fragmentary specimens recently discovered by S. Wood in the Reservoir Formation may belong to this species.

Diagnosis. A species of *Eskaspis* lacking connection between the subfrontal depressions of the anterior region of the doublure and the posterior, notched portion of the vincular furrow. Eyes large, with nineteen files (rarely eighteen in adults) with a general lens formula of 565 787 877 765 543 2 and about 116 lenses in all. Smaller specimens (approximately half adult size), with eighteen files of no more than six lenses. Lowermost lenses very small, elliptical in some specimens.

Dimensions. Holotype: total length (sag.) 20.0 mm, cephalic length (sag.) 5.7 mm, width 13.0 mm. Range in cephalic length 2.2–9.0 mm, width 5.0–17.5 mm.

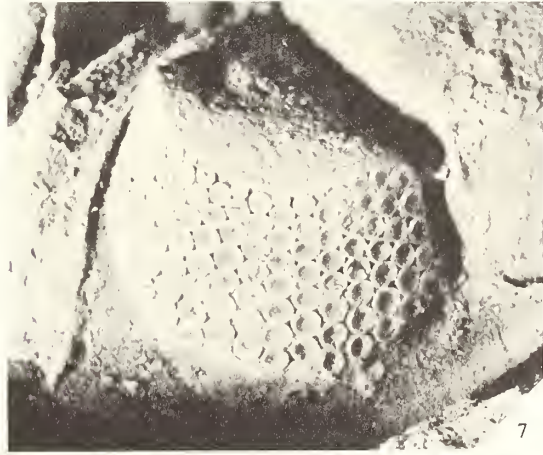
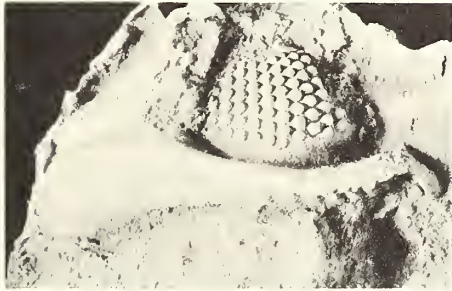
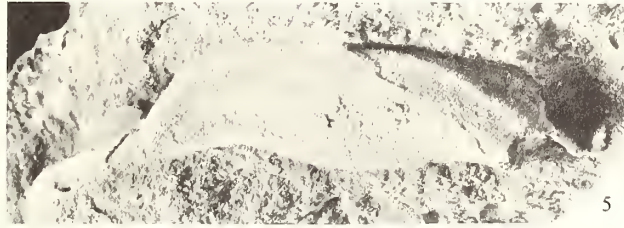
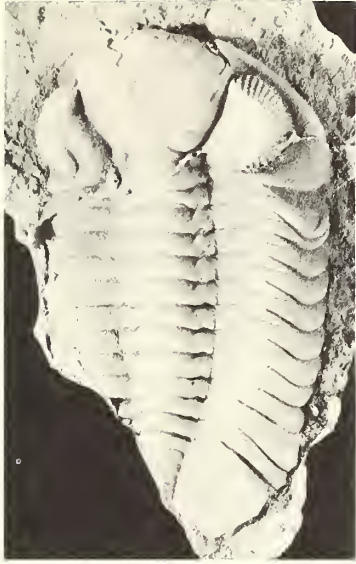
Description. Cephalon relatively broad, width/length ratio being approximately 2:1, and with an almost rounded (subangular) anterior margin (text-fig. 2a). Glabella half the cephalic width at its widest, broadly heptagonal, expanding anteriorly, widest in front of eyes where it is about as broad as its length. Glabellar crown (in profile) slightly higher than palpebral lobes (text-fig. 2d). In lateral profile the glabella is rather flattened on top, but slopes with increasing steepness to meet the anterior margin at about 80° with no real preglabellar furrow or preglabellar field, so that the glabella is directly in contact with the cephalic doublure. Axial furrows moderately deeply impressed, running forwards from lobe 1p at about 45° to an exsagittal line and changing direction where the palpebral furrow contacts glabellar lobe 3p, thence diverging from the exsagittal line only by some 10°, its course being indented slightly by the anterior edge of the eye. Axial nodes small, usually round but sometimes elongate.

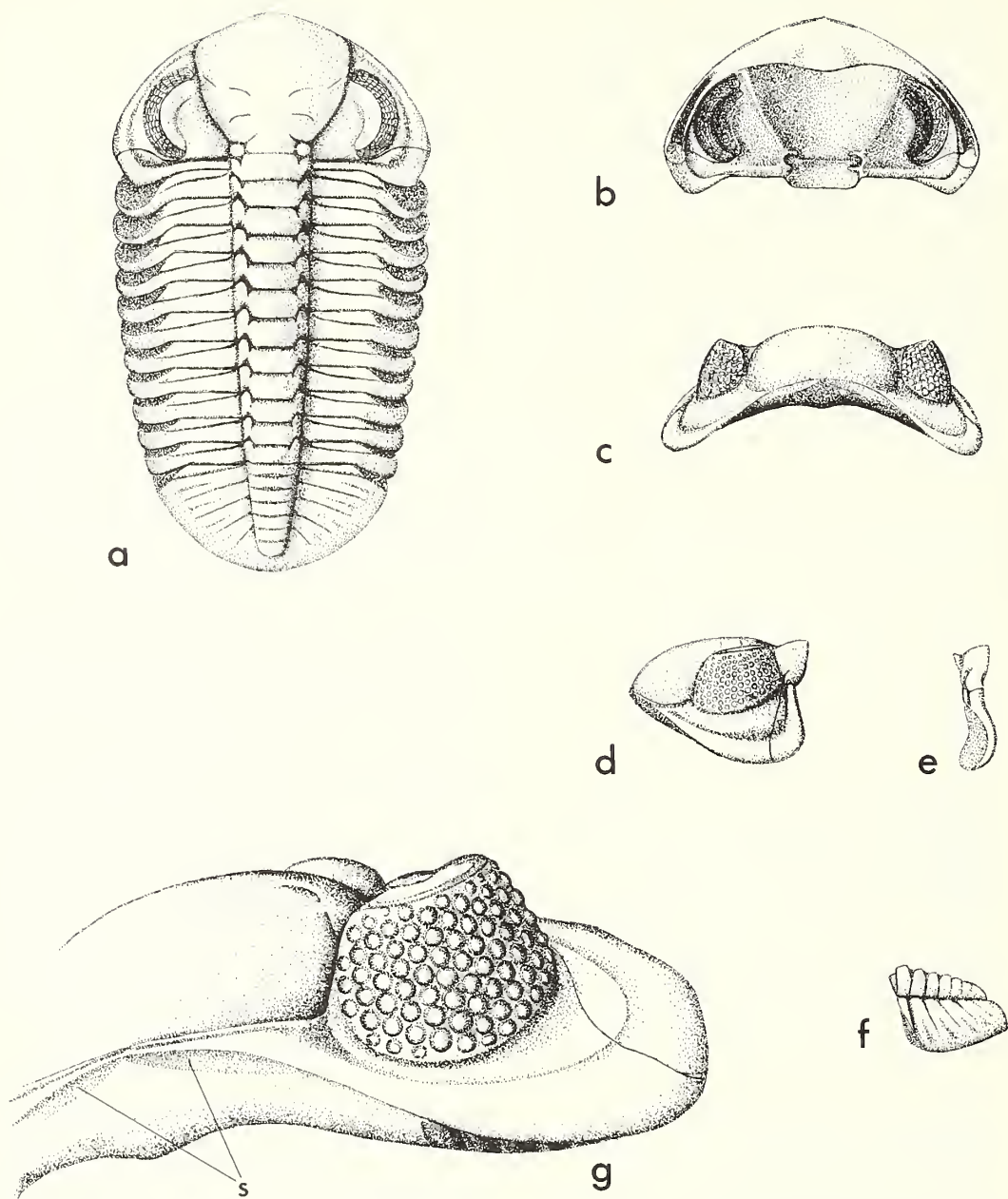
All glabellar furrows faintly impressed and approximately equidistant from one another. 1p is the deepest; it is discontinuous and anteromedially directed at 45°.

EXPLANATION OF PLATE 18

Figs. 1–9. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Wether Law Linn Formation (Telychian), North Esk Inlier, Pentland Hills. 1, neotype. Wether Law Linn (WL), IGS 1035,* × 3.5. 2, complete specimen. Deerhope Burn (DB), Gr. I. 40282,† × 2.3. 3, almost complete, somewhat disarticulated specimen (DB), Gr. I. 40279,† × 2.5. 4, partially enrolled specimen (WL), IGS 5783,* × 3.5. 5, anterior doublure, showing subfrontal depressions, antero-ventral view (WL), Gr. I. 40269,* × 4.5. 6, eye and vincular notches, ventro-lateral view, Gr. I. 40270,* × 5. 7, right eye, Gr. I. 40279,† × 10. 8, doublure (cf. text-fig. 3) (DB), Gr. I. 40262,* × 5. 9, almost complete specimen in lateral view (DB), Gr. I. 40281,† × 4.

* Latex replica of external mould. † Internal mould.





TEXT-FIG. 2. *Acernaspis (Eskaspis) sufferta* (Lamont). Reconstructions of *a*, whole animal in dorsal view. *b-d*, cephalon in ventral, frontal, and lateral view. *e*, thoracic segment showing facet in lateral view. *f*, pygidium in lateral view. *g*, cephalon in oblique lateral view, showing subfrontal depressions (*s*). *a-f*, $\times 3.5$; *g*, $\times 8.5$.

Furrow 2p nearly transverse with the outer tip recurved; 3p in two distinct unjoined parts, inner part directed slightly forwards, outer part at 45° and not reaching the axial furrow. Intercalating ring not sharply demarcated anteromedially, but confluent with composite glabellar lobes. Anterior lobe half the total length of the glabella. Auxiliary glabellar impressions form a circular pattern, some are quite deeply impressed (text-fig. 5) (cf. *Acernaspis* figured by Eldredge 1971, text-fig. 2j).

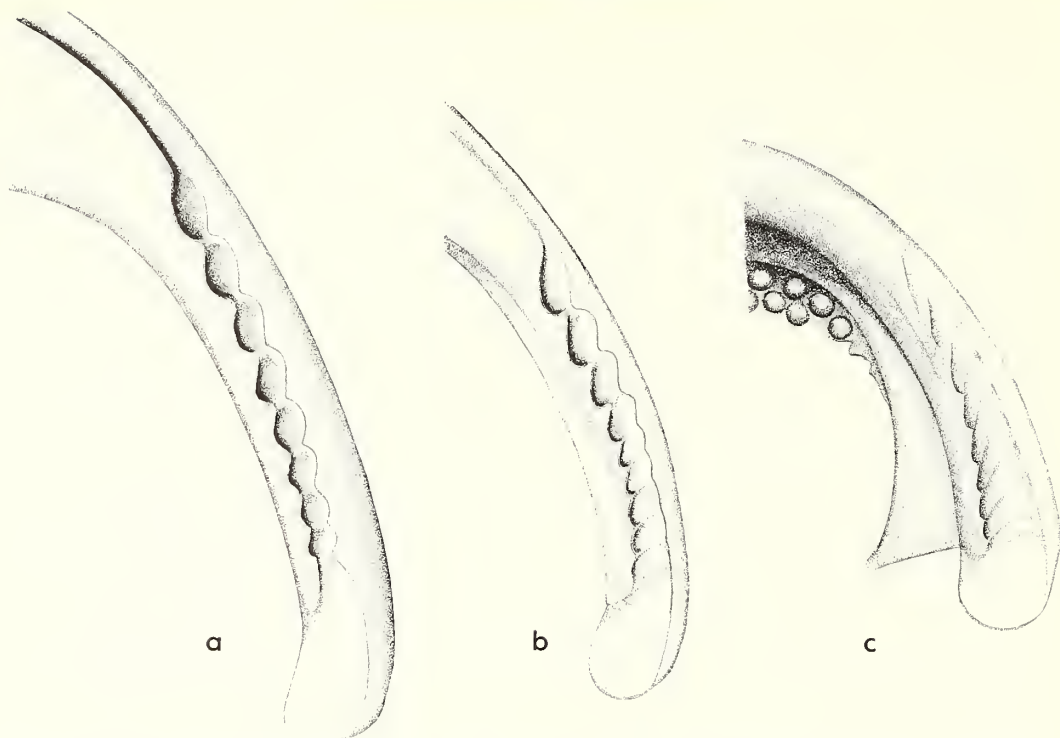
Occipital furrow straight and shallow medially, more deeply impressed laterally, at the apodemal pit, occipital ring very large (as wide as the posterior part of the glabella including lateral nodes) and with prominent lateral lobes directed forwards and outwards at 45° . Genal region with a definite lateral border which is widest postero-laterally, and delimited by a broad, shallow, lateral border furrow, less distinct below the eye, but becoming more incised anteriorly and nearly reaching the glabella. Posterior border furrow straight and deeply incised. Genal angles truncated, projecting somewhat posteriorly and subangular.

Palpebral lobes large, slightly inflated, and with a faint external rim extending from furrow 3p to the occipital furrow. Palpebral furrow usually distinct though may be rather vaguely defined in the central part. Palpebral area quite broad, triangular, mainly flat or slightly inflated. Eyes very large, nearly half the total height of the cephalon, the posterior edge slightly further from the midline than the anterior (Pl. 18, fig. 7; text-fig. 1g).

Lenses projecting beyond the sclera, not sunken, arranged in nineteen dorso-ventral files (commonly eighteen in juveniles but rarely in adults) with a general lens formula:

567 787 877 765 543 2. Maximum per file eight. Total 116.

In some specimens the lowermost lenses are very small and elliptical. Eye socle very reduced. Facial suture apparently functional in holaspids, the anterior branch cutting antero-lateral corners of the anterior face of the glabella, meeting at a distinct point on the midline. Posterior branch directed at first anteriorly, then curving outwards and backwards again to reach the border opposite the posterior edge of the eye. The suture appears again on the postero-lateral part of the doublure making a posteriorly convex, symmetrical U-shaped lobe behind the course of the dorsal part of the suture (text-fig. 3). Cephalic doublure nearly a third the length of the glabella sagittally its rear margin convex posteriorly, the central part convex downwards. Vincular furrow marked anteriorly only as a pair of elongate, contiguous, and shallow subfrontal depressions on either side of the midline (text-fig. 1b, g (marked 's')). Where the depressions meet, there is a tiny forwardly projecting point. Subfrontal depressions separated from the notched lateral vincular furrow which extends from below the anterior edge of the eye to nearly below its posterior edge. The inner lamella of the lateral doublure is less steeply inclined in lateral aspect than the outer lamella which forms the postero-lateral margin of the cephalon. Posteriorly, the inner lamella ends abruptly below the dorsal facial suture in front of the U-shaped lobe; the outer lamella extends further back (text-fig. 3). The most anterior notches are less deeply impressed than those which lie posteriorly; nine notches are evident in all, and are arranged radially from a point posterior to the U-shaped lobe defined by the doublural suture. The doublure turns abruptly at the



TEXT-FIG. 3. The lateral part of the ventral doublure, showing vincular structures and coaptative morphology in *Acernaspis* (*Acernaspis*) and *A. (Eskaspis)*. *a*, *A. (Acernaspis) elliptifrons* (Esmark), from the Newlands Formation (Idwian), Girvan, Ayrshire. BM 1t 9121. *b*, *A. (Eskaspis) woodburnensis* n. sp. from Wood Burn Formation (lowermost Telychian), Lauchlan Burn, Girvan, Ayrshire. IGS 5777. *c*, *A. (Eskaspis) sufferta* (Lamont), Wether Law Linn Formation (upper Telychian), Pentland Hills, near Edinburgh. Gr. 1. 40262 (see Pl. 18, fig. 8), all $\times 14$. All these illustrations are camera-lucida drawings made from latex replicas of external moulds.

genal angle and tails off to terminate just behind the posterior edge of the eye. Occipital and 1p apodemes distinct on ventral surface of the cephalon.

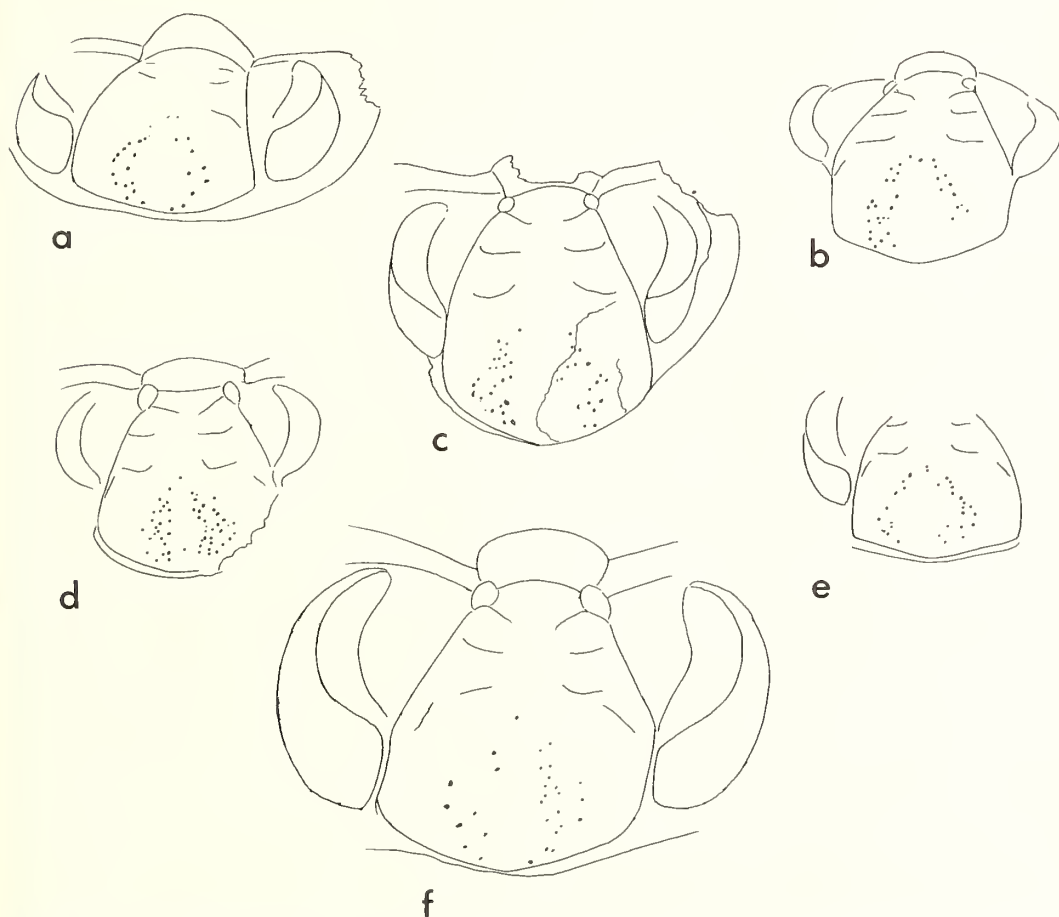
Thorax of eleven segments tapering backwards slightly, having quite strongly arched rings. Axis is quarter the total width. Each axial ring is indented anteriorly by deep paired incisions, which together with shallower posterior incisions placed closer to the axial furrows delimit chevron-shaped axial lobes, set further forward than the axial part of the ring but are not swollen as nodes (text-fig. 2*a*, *e*). Posterior border of each axial ring high and sharp. A distinct furrow divides the articulating half-ring from the axial ring.

Pleural regions flat but strongly bent down distally. Pleural furrows straight or slightly curving, narrow, of moderate depth, and extend as far as the articulating facets. Facets very pronounced anteriorly while the pleural ribs are very narrow and curved, but diminishing in size and curvature posteriorly. The rear edge of the flat top of each pleuron has a narrow flange articulating with a corresponding anterior groove on the next segment.

Pygidium with rounded or almost imperceptibly pointed margin with nine to ten rings diminishing in size posteriorly (text-fig. 2*a, f*). The last two axial rings are indistinct, the first three or four have a pseudo-articulating half-ring. There are four or five pleural furrows whose obliquity increases backwards, the first being quite deep, the others increasingly shallow, interpleural furrows weakly impressed, and disjunct. All pleural and interpleural furrows fade out some distance before the pygidial margin, leaving a broad smooth border zone.

Pygidial doublure broad, with two lateral parts forming a small notch in the sagittal line and shaped to fit the two vincular depressions on the cephalon.

All parts of the exoskeleton are covered with dense microgranular sculpture except for the subocular groove which is smooth. On the doublure, glabella, and axial rings and pleural ribs this sculpture is especially dense, though it is sparser on the flat tops of the pleurae.



TEXT-FIG. 4. *Acernaspis* (*Eskaspis*) *sufferta* (Lamont). Camera-lucida drawings showing auxiliary impression patterns on the anterior glabellar lobe. All $\times 5$. *a*, Gr. I. 40271; *b*, Gr. I. 40263; *c*, Gr. I. 40281; *d*, Gr. I. 40265; *e*, Gr. I. 40264; *f*, Gr. I. 40257.

Acernaspis (Eskaspis) woodburnensis, n. sp.

Plate 19, figs. 9, 11–13; text-fig. 5a, b

1899 *Phacops stokesi* (M.-Edw.). Peach and Horne, p. 538.1906 *Phacops elegans* Sars and Boeck. Reed, p. 155.*Locus typicus*. Lauchlan Burn (Bargany Pond Burn, Girvan, Ayrshire).*Stratum typicum* (Wood Burn Formation, lowermost Telychian) (Cocks and Toghill 1973, p. 225)

Diagnosis. Axial furrows straight, diverging forwards to a point in front of the eye. Eyes fairly large, not particularly high, posterior edge more distant than the anterior edge from the sagittal line. Lenses distributed in sixteen files as follows:

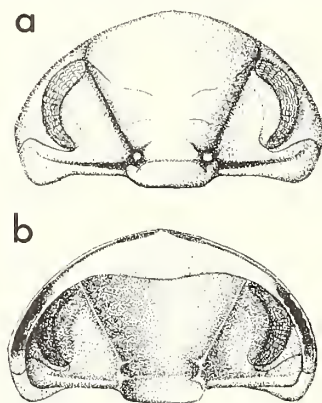
566 677 776 766 534 3. Maximum per file seven. Total 90.

Posterior section of doublure has ?nine vincular notches on each side connected by a shallow vincular furrow to the subfrontal depressions.

Types. Holotype IGS 5777. Paratypes IGS 5778–5779, 5780–5781 (parts and counterparts).

Other material. Ten specimens in IGS collections.

Remarks. *A. (E.) woodburnensis* is the oldest member of this subgenus known at present but is stratigraphically younger than the middle Llandovery *A. (A.) elliptifrons* of the Newlands Formation. It is particularly interesting that here a



TEXT-FIG. 5. *Acernaspis (Eskaspis) woodburnensis*, n. sp. a, b, cephalon reconstructed in dorsal and ventral view, $\times 2.25$.

EXPLANATION OF PLATE 19

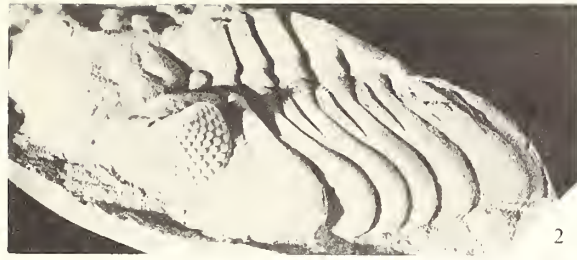
Figs. 1–7, 10. *Acernaspis (Eskaspis) sufferta* (Lamont). Wether Law Linn Formation (Telychian), North Esk Inlier, Pentland Hills. 1, cephalon with auxiliary impression patterns, Gr. I. 40257, * $\times 3.5$. 2, cephalon and part thorax, oblique anterolateral view, Gr. I. 40243, * $\times 3.75$. 3, almost complete specimen, oblique antero-lateral view, Gr. I. 40281, † $\times 5.25$. 4, pygidium, Gr. I. 40260, * $\times 6$. 5, almost complete enrolled specimen, Gr. I. 40280, † $\times 2.75$. 6, genital point, visible only on internal mould, Gr. I. 44093, † $\times 15$. 7, small cephalon, Gr. I. 40261, † $\times 4$. 8, almost complete specimen, Gr. I. 40275, * $\times 3.75$. 10, doublure of small specimen, Gr. I. 44094, † $\times 5.5$.

Figs. 9, 11–13. *A. (Eskaspis) woodburnensis*, n. sp. Wood Burn Formation (lowermost Telychian). 'Bargany Pond Burn' = Lauchlan Burn, Maxwellton Hill, Girvan. 9, ventral view of holotype cephalon showing doublure with shallow furrow connecting vincular notches to subfrontal depressions, IGS 5777, $\times 3.5$. 11, holotype, IGS 5777, † $\times 2.5$. 12, 13, anterior and dorsal views of complete specimen retaining its cuticle though altered and exfoliated in places, IGS 5780, $\times 2$.

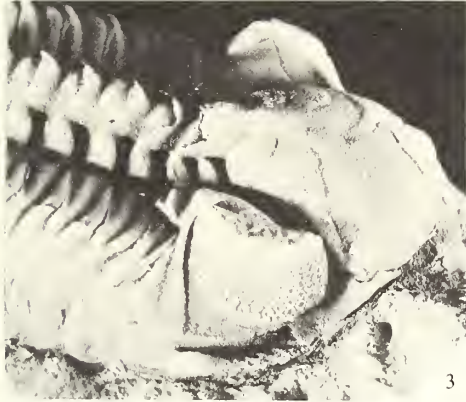
* Latex replica of external mould. † Internal mould.



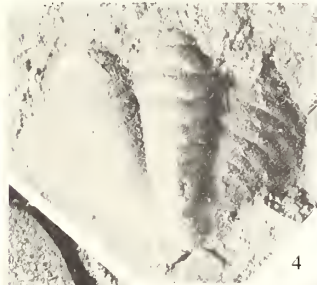
1



2



3



4



5



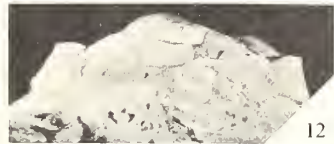
6



10



7



12



8



11



13

shallow vincular furrow is present, though absent in the otherwise quite similar *A. (E.) sufferta*.

Dimensions. Holotype: total length (sag.) 28.0 mm, cephalic length (sag.) 10.0 mm, width 18.5 mm. Range in cephalic length 9.5–11.0 mm, width 17.0–20.0 mm.

Superfamily DALMANITACEA Vogdes, 1890

Family PTERYGOMETOPIDAE Reed, 1905

Genus *PODOWRINELLA* gen. nov.

Type species. *Podowrinella straitonensis* (Lamont, 1965) by original designation and monotypy, from the Knockgardner Formation (?Wenlock) of the Blair-Straiton district near Girvan, Ayrshire, and the Ree Burn Formation (?Telychian, upper Llandovery), Hagshaw Hills, and the Deerhope Formation (Telychian), North Esk Inlier, Pentland Hills.

Etymology. From the Podowrin Burn in the Hagshaw Hills where the Ree Burn Formation outcrops and where fossils are common in the turbidites.

Diagnosis. Small Phacopina combining features of both phacopid and pterygometo-
pid organization. Cephalon roughly triangular but with truncated genal angles. Glabella pear-shaped with furrow 1p connected to 3p as in Pterygometo-
pidae but 3p in two distinct parts as in Phacopidae, and confluent with axial furrows. Eyes
with about eighteen files with up to seven lenses each, about 100 lenses altogether. Cephalic
doublure traversed by deep, broad coaptative grooves, continuous laterally, becoming dorso-
medial just before they meet. Thorax with axial nodes and strongly downturned outer parts
of the pleurae. Pygidium somewhat triangular with a rounded or occasionally slightly pointed
margin.

Podowrinella straitonensis (Lamont, 1965)

Plate 20, figs. 1–14; text-fig. 6a–h

1962 *Phacops* sp. nov. Rolfe, p. 252.

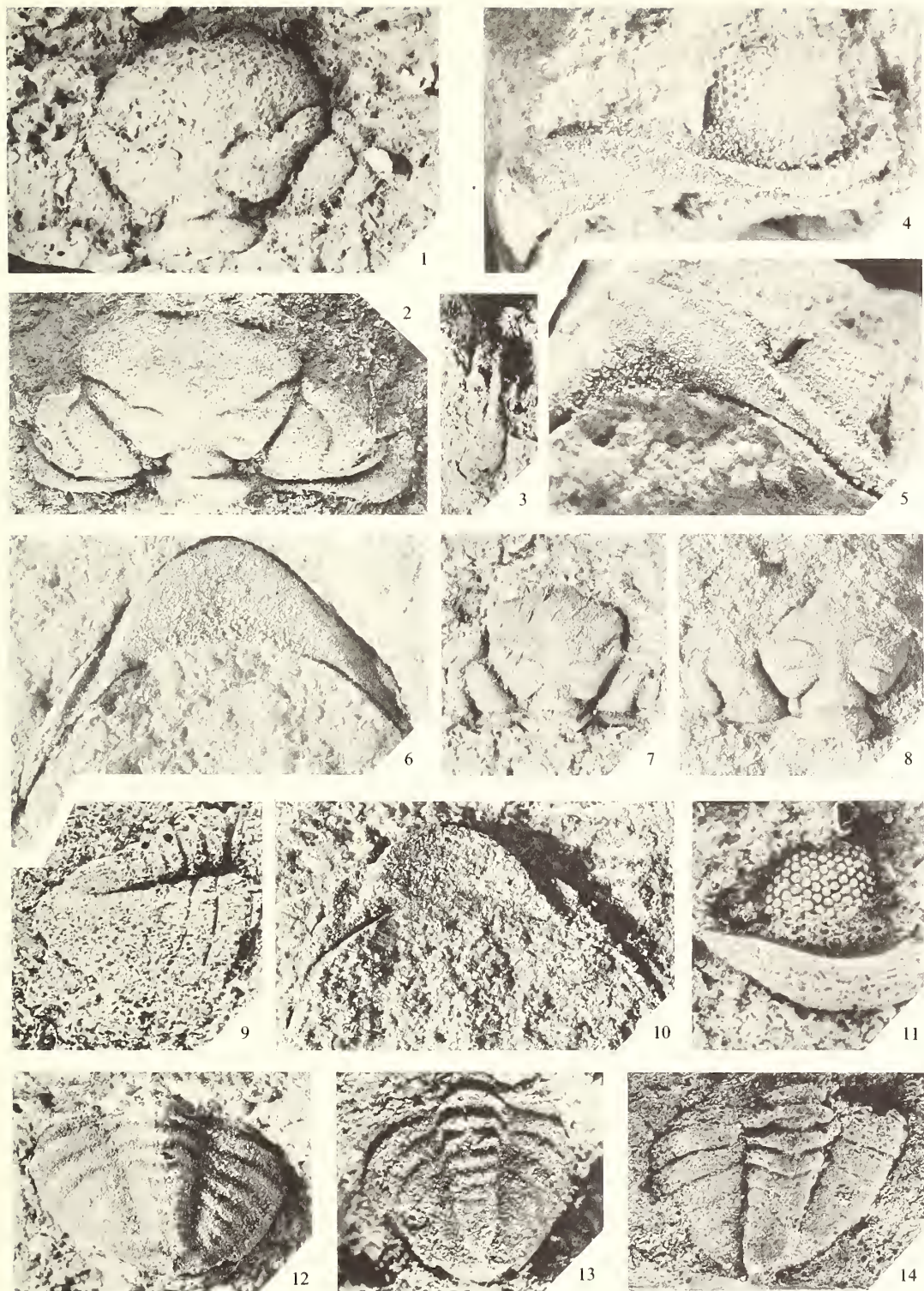
1965 *Phacops straitonensis* sp. nov. Lamont, p. 39, pl. V, fig. 5.

1973 *Phacops straitonensis*. Rolfe, p. 109.

EXPLANATION OF PLATE 20

Podowrinella straitonensis (Lamont). 1, neotype cranidium, figured by Lamont (1965, pl. V, fig. 5), almost undistorted. Ree Burn Formation, Hagshaw Hills (Rolfe's loc. 31), BU 1900,* $\times 6$. 2, cranidium in W-mode deformation. Top of Deerhope Formation, Deerhope Burn, North Esk Inlier, Pentland Hills (locality B), Gr. I. 40340,* $\times 5.5$. 3, thoracic segment in lateral view. Pentland Hills (loc. B), Gr. I. 40348,† $\times 3.5$. 4, 5, anterolateral and ventrolateral view of detached librigena showing vincular furrows and eye, small quarry in the Ree Burn Formation, nearly opposite junction of Shiel Burn with Monk's Water, Hagshaw Hills (loc. A), RSM 1975-43-2,† $\times 6.5$. 6, ventral surface showing vincular furrows, RSM 1975-43-3,† $\times 6$. 7, undistorted cranidium. Knockgardner Formation, Knockgardner, IGS M 13219,† $\times 3.5$. 8, cranidium. Pentland Hills (loc. B), Gr. I. 40310,* $\times 5.55$. 9, lateral view of compressed pygidium. Pentland Hills (loc. B), Gr. I. 40345,* $\times 7.5$. 10, ventral surface W-mode deformation. Pentland Hills (loc. B), Gr. I. 40358,† $\times 6$. 11, left eye and subjacent librigena. Hagshaw Hills (loc. A), RSM 1975-43-4,* $\times 7.5$. 12, pygidium. Hagshaw Hills (loc. A), RSM 1975-43-5, $\times 5.5$. 13, pygidium (L-mode deformation). Pentland Hills (loc. B), Gr. I. 40349,* $\times 5$. 14, pygidium showing accessory half-ring on segment 1. Pentland Hills (loc. B), Gr. I. 40307,* $\times 6.5$.

* Latex replica of external mould. † Internal mould.



CLARKSON, ELDREDGE and HENRY, *Podowrinella*

*Material**(a) Hagshaw Hills.*

(1) Twenty-five specimens from the Rolfe Collection, University of Birmingham, including BU 1900a, b figured by Lamont (1965, pl. V, fig. 5), which is herein designated as neotype, since the unfigured holotype from Knockgardner is now lost (Lamont pers. comm.).

Neotype. BU 1900a, b (from Rolfe's locality 31/48 in unpublished thesis; University of Birmingham 1960).

Other material. Thirty other specimens in the collection of the Department of Geological Sciences, University of Birmingham.

(2) One hundred specimens from the Ritchie Collection, Royal Scottish Museum, collected from a small quarry in the Ree Burn Formation on the east bank of the Monk's Water, opposite the mouth of the Shiel Burn, Hagshaw Hills. These include the paratypes RSM 1975-43-1, RSM 1975-43-2 (Pl. 20, figs. 4, 5), RSM 1975-43-3 (Pl. 20, fig. 6), RSM 1975-43-4 (Pl. 20, fig. 11), RSM 1975-43-5 (Pl. 20, fig. 12).

Also twenty-five RSM specimens from the foot of the Podowrin Burn, east of Monk's Water, Hagshaw Hills.

In addition, fifty-five other specimens from the same localities in the Grant Institute Collections (Gr. I.).

(b) North Esk Inlier. Specimens from Tipper and Clarkson Collections. Top of Deerhope Formation, Deerhope Burn. Paratypes Gr. I. 40340, Pl. 20, fig. 2; Gr. I. 40348, Pl. 20, fig. 3; Gr. I. 40310, Pl. 20, fig. 8; Gr. I. 40348, Pl. 20, fig. 9; Gr. I. 40358, Pl. 20, fig. 10; Gr. I. 40349, Pl. 20, fig. 13; Gr. I. 40307, Pl. 20, fig. 14.

(c) Knockgardner. Blair-Straiton Inlier, east of Girvan. Maconochie Collection. IGS M 13219 (Pl. 20, fig. 7) and twenty-five other IGS specimens. Also thirty specimens in Grant Institute of Geology.

Range. Telychian (North Esk, Hagshaws)—?lower Wenlock (Knockgardner).

Remarks. The material available from Knockgardner and the Hagshaw Hills is all preserved as disarticulated fragments collected from the base of turbidite flows. Specimens are found in all orientations and most individuals have suffered some distortion. The notable variation in width and length between specimens resembling the L and W forms of Henningsmoen (1960, p. 207) and Sadler (1974, pp. 81, 85) is attributed to stress due to crushing pressure of the mass of unconsolidated turbidite after deposition. Some sheared specimens occur also. The reconstructions were made from the less distorted specimens.

Dimensions. Holotype: cephalic length (sag.) 5 mm, width 10 mm. Range in cephalic length 4-6 mm, width 8-12 mm.

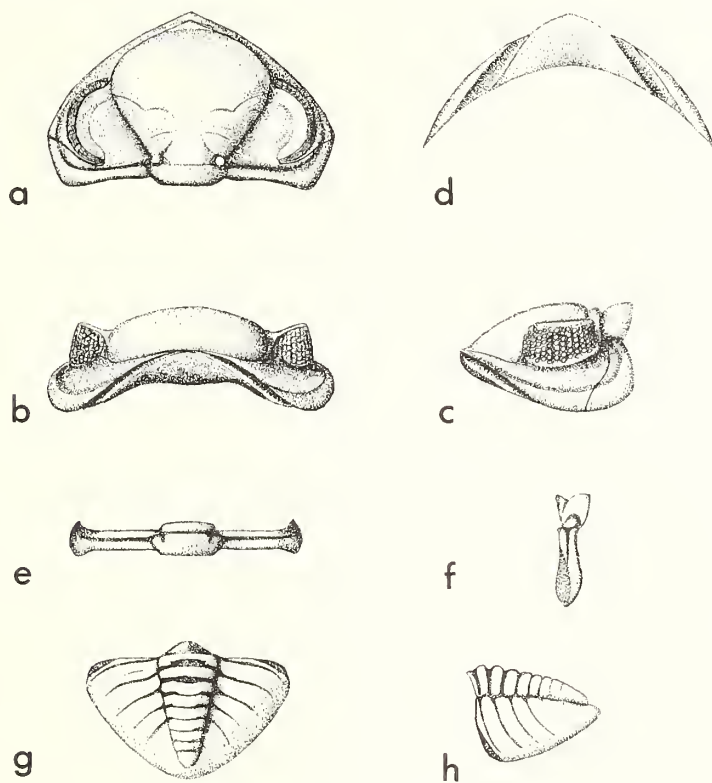
Description. Small Phacopidae with roughly triangular cephalic outline (in dorsal view), modified by truncated genal angles. Cephalon widest at distal librigenal/fixigenal junction. In lateral view (text-fig. 6c) (in standard orientation), glabella depressed anteriorly, sloping regularly postero-dorsally, with central region of glabella extending above level of palpebral lobes. Large anterior arch developed in frontal view.

Axial furrows moderately deeply implaced, diverging at an angle of approximately 65° then abruptly reflected directly in front of the anterior edge of the palpebral lobe, and curving smoothly around anterior glabellar lobe, becoming confluent with anterior and lateral cephalic border furrows.

Glabella pear-shaped, with anterior, 3p, 2p, and medial portion of 1p lobes united to form composite glabellar lobe (text-fig. 6a). Anterior glabellar lobe sub-ovate, continuous with medial portion of remainder of glabella. Anterior margin of anterior glabellar lobe rounded, bounded by furrow bearing anterior ramus of

facial suture antero-laterally. Facial suture continuous with anterior border furrow medially; anterior border, border furrow, and facial suture thus meeting in a distinct point medially, delimiting a small, triangular pre-glabellar field proximal to facial suture. Anterior border thin, though distinct in front of this field; concentric with facial suture, but disappearing marginally.

Glabellar furrow 3p in two parts, with sharp bend between distal and proximal branches; branches generally connected at bend by shallow furrow, occasionally



TEXT-FIG. 6. *Podowrinella straitonensis* (Lamont). *a-c*, reconstructions of cephalon in *a*, dorsal, *b*, frontal, *c*, lateral aspects. *d*, cephalic doublure in ventral view. *e*, *f*, thoracic segment in dorsal and lateral view. *g*, *h*, pygidium in dorsal and lateral view. All $\times 4$.

wholly disconnected on internal and external moulds. Distal branch of 3p furrow deepest proximally, confluent with axial furrow just opposite anterior margin of visual surface, slightly convex anteriorly, running at an angle of approximately 55° from the midline. Proximal branch of 3p furrow comma-shaped, with proximal terminus slightly posterior to distal terminus. Proximal terminus continuous with a broad, shallow, variably developed longitudinal glabellar furrow running posteriorly and communicating smoothly with 1p glabellar furrows. Glabellar furrow 2p short, comma-shaped (convex anteriorly) with distal and proximal tips in transverse line, and not communicating with axial furrow distally, but confluent with

longitudinal glabellar furrow medially. Glabellar furrow 1p deeply incised distally, confluent with axial furrow, and recurved antero-proximally. Glabellar furrow 1p apparently continuous medially as broad, shallow furrow, delineating an intercalating ring.

Glabellar lobe 3p hypertrophic distally; ratio of glabellar lobe lengths along axial furrow roughly: 4.7:2:1 for 3p:2p; 1p. 2p lobe small, ovate, 1p lobe longest medially, reduced to nodes distally, and depressed below concordant surface of anterior glabellar region and occipital ring. Occipital furrow shallow, straight; occipital ring of approximately equal length (sag.) throughout.

Posterior border furrow shallow, communicating with axial furrow, running nearly transversely, distally becoming more shallow and recurved antero-distally, confluent with lateral border furrow of librigena. Posterior border distinct, roughly transverse proximally, becoming thickened distally near genal margin, thereby causing slight deflection to posterior margin of cephalon. Posterior border sharply reflected antero-distally, forming a bluntly pointed genal angle of approximately 100°. Lateral cephalic border reflexed antero-proximally at point where crossed by posterior ramus of facial suture. Lateral border continuous with anterior border; anterior border becoming progressively thinner approaching midline.

Lateral border of librigena steeply inclined, capped by sharp ridge; lateral border furrow broad, smoothly confluent with concave distal portion of librigena (text-fig. 6c). Librigena becoming steeply inclined proximally, merging with eye socle (not distinctly defined because of lack of ornamental features due to poor preservation). Visual surface nearly vertical, with eighteen d-v files with up to seven lenses per file, about 100 lenses in all. Eye moderately long, not reaching posterior border furrow. Palpebral lobe quite narrow, inflated above palpebral area and set off from it by a sharply implaced palpebral furrow. Palpebral area relatively flat, sloping postero-proximally and smoothly confluent with fixiginal area posterior to eye.

Cephalic doublure produced anteriorly into flat trapezoidal spatulate process, inclined at an angle of approximately 25° (in lateral view) and visible in frontal view. Spatulate process bounded distally by deep, broad grooves traversing doublure, and inclined antero-proximally at an exsagittal angle of approximately 35°. Grooves continuous laterally, becoming dorsal where converging at midline (text-fig. 6b, d). Anterior-most medial portion of cephalon a thin ridge where anterior border, vincular groove, and spatulate process coterminate. Cephalic doublure developed as thin ridge postero-distally to vincular grooves; inner wall nearly vertical. Hypostoma unknown.

Auxiliary impression pattern and details of cephalic ornament unknown; cephalon apparently smooth (based on study of external moulds).

Thorax incompletely known; most of the thoracic segments examined (probably the anterior ones) with the axis one-quarter the width of the whole, axial nodes set off by short, deep anterior furrows (text-fig. 6e, f). Pleural furrows relatively shallow, of moderate depth, and straight. Inner part of pleura flat, outer third sharply turned down; pleural tips pointed. Pleural facets present but not very distinct.

Pygidium (text-fig. 6g, h) equilaterally triangular with, however, its posterior apex truncated, having approximately eight axial rings and terminal piece; two or more accessory half-rings present. Axis not reaching posterior pygidial margin, acutely

rounded posteriorly. At least four pairs of pleurae present; inter-pleural furrows obscure. Pleural furrows becoming fainter posteriorly, and nowhere reaching pygidial border. Most specimens have a rounded pygidium, but in some examples the posterior border is slightly pointed, especially in those from the Pentland Hills.

Remarks. This genus cannot be readily confused with any other taxon known to us. To clarify its diagnosis and to aid in recognition of related forms we briefly discuss which features are peculiar to the taxon alone, and which are 'phacopid-like' and 'pterygomotopid-like'.

There is no question that *Podowrinella* is, in the great majority of its features, pterygomotopid in aspect. In fact, *Podowrinella* is very similar indeed to the Ordovician pterygomotopids *Calyptaulax* and *Eonouarachus*, in particular to those species of *Calyptaulax* from Europe which, as Shaw (1974, p. 42) has noted, have a 'noticeable bend' along glabellar furrow 3p. Pterygomotopid-like features of *Podowrinella* include over-all conformation of cephalon; possession of a distinct lateral and anterior border (reduced anteriorly in *Podowrinella*); glabellar segmentation, generally, including size and shape of glabellar lobes and presence of longitudinal glabellar furrows; narrow palpebral lobes; anterior branch of facial suture meeting in a distinct point; presence of a spatulate medial projection of the cephalic doublure; and a somewhat triangular pygidium, pointed in some examples.

Podowrinella is phacopid-like in the following features: presence of a 3p glabellar furrow divided into two parts, discontinuous in some specimens of *P. straitonensis*, with the proximal moiety nearly transversely oriented (the distal ramus remains pterygomotopid-like in conformation); a smoothly rounded anterior glabellar margin; truncated genal angles, without genal spines; nearly complete loss of inter-pleural furrows, and sharp reduction in the number of pleural furrows, on the pygidium. We hasten to add that some species of *Calyptaulax*, particularly *C. callicephala*, are very much like *Podowrinella* in having a smoothly rounded anterior glabellar margin and truncated genal angles; supposed 'phacopid-like' characters. Finally, *Podowrinella* appears to be rather unique in the coaptative doublure morphology, though some pterygomotopid species, again, particularly *C. callicephala*, are somewhat similar in possessing a vincular furrow traversing the doublure and converging antero-dorsally at the midline.

Though we have been unable to reach a final agreement on the taxonomic position of *Podowrinella*, the unusual combination of characters which it displays does reinforce Eldredge's (1971) suggestions as to a close relationship between Phacopidae and Pterygomotopidae. There are some interesting resemblances between *A. (Eskaspis)* and *Podowrinella*, in terms of glabellar furrowing, eye size and position, and genal angles. Sometimes specimens of *A. (E.) sufferta* show traces of extended glabellar furrows, so that 1p and 3p are faintly connected (e.g. the slightly crushed specimen in Pl. 19, fig. 1). There seem to be possible grounds for restructuring the current classification of Phacopina and the curious morphology of *Podowrinella* could be critical.

Coaptative structures in A. (Acernaspis), A. (Eskaspis), and Podowrinella: some remarks

Within trilobites of the Phacopina and other suborders there have been described a substantial array of structures on the ventral doublure of the cephalon which interlock during enrolment with mirror-image structures on the thorax and the pygidium. Examples have been figured by Campbell (1967), and others have been discussed in detail by Henry and Nion (1970), Clarkson and Henry (1973), and Henry and Clarkson (1975). These have arisen independently in a number of trilobite groups and have been defined (Hupé 1953; Clarkson and Henry 1973) as coaptative mechanisms. They have, in our estimation, much potential value in taxonomy, as well as their intrinsic interest from the functional and evolutionary point of view, but before this can be effectively realized, it is essential to illustrate and document the various types present in different trilobite groups.

This study gives information of the nature of coaptative mechanisms of *A. (Acernaspis)*, *A. (Eskaspis)*, and *Podowrinella*. In *A. (Eskaspis)* (text-fig. 3c) there are nine vincular notches on each side which receive the tips of the thoracic pleurae. Though no complete enrolled specimens have been found which might enable further details of the mechanism to be elucidated, it appears that these notches are for the reception of the last nine pleural tips; the first two pleurae are shorter and have wider facets. During enrolment, they probably locked in against the end of the inner ridge of the doublure (text-fig. 3) close together with the tip of the third pleuron. The more posterior pleurae were fitted into depressions which became progressively more spaced out towards the anterior of the doublure, whilst becoming less deeply impressed. By contrast with *A. (Acernaspis)* which has a well-marked semicircular vincular furrow connecting the two lateral sets of vincular notches (text-fig. 3a), *A. (E.) woodburnensis* has only a very shallow furrow, connecting with the two subfrontal depressions, whilst *A. (E.) sufferata* only has the two depressions, and no furrow at all. In both species of *A. (Eskaspis)* two slightly swollen areas on the pygidial doublure fit into the subfrontal depressions; otherwise the pygidium comes to rest freely against the flat (or only slightly indented in the case of *A. (E.) woodburnensis* surface of the anterior part of the cephalic doublure. This difference between the coaptative morphology of the doublure of *A. (Acernaspis)* and *A. (Eskaspis)* is coupled with the fact that in the former subgenus the surfaces of the parallel vincular ridges lie in the same plane, whereas in the latter they are somewhat oblique to one another, so that the inner ridge as seen in lateral profile having the higher angle to the horizontal; there are other differences also as previously mentioned (p. 125). It is not certain whether the morphological sequence illustrated in text-fig. 3, and previously referred to is a true evolutionary sequence. Had the specimens all been collected from a single vertical section it would be almost unequivocal. Even so, the morphology, confined distribution, and stratigraphically sequential changes suggest a definitive evolution towards the grade of organization in *A. (E.) sufferata* within a fairly localized area.

Podowrinella has no separate notches for the reception of individual pleural tips, but only a pair of elongated furrows, deepening posteriorly and becoming slightly twisted in the process. With this type of structure the pleural tips come to rest in the groove, as does the doublure of the pygidium, and presumably the triangular point

at the extreme anterior of the cephalon forms a seal with the similarly angular sagittal edge of the said pygidial doublure. Such coaptative morphology resembles that of some Pterygometopidae though in a more extreme form.

The range in morphology of coaptative structures amongst Phacopina is considerable; compare, for example, the ventral morphology of the doublure in *Kloucekia*, *Morgatia*, and *Crozonaspis* species (Henry and Nion 1970; Clarkson and Henry 1973), with that of the trilobites discussed in this paper. The value of these in taxonomy is probably very great, but there is, as present, a need for detailed study covering a wider spectrum than is presently known, and only then will their actual value be able to be established.

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EVOLUTION OF THE CHAROPHYTE FLORAS IN THE UPPER EOCENE AND LOWER OLIGOCENE OF THE ISLE OF WIGHT

by MONIQUE FEIST-CASTEL

ABSTRACT. The distribution of charophyte gyrogonites in the Headon, Osborne, and Bembridge Beds is analysed. The flora, including a new species, *Nitellopsis (Tectochara) latispira*, is described. It is considered that transitional forms in the genera *Psilochara* and *Harrisichara* constitute examples of evolution in Palaeogene genera. The stratigraphical importance of *Sphaerochara subglobosa* (Groves) Horn af Rantzen, which extends from the Upper Headon to the Lower Hamstead Beds, is discussed. It is confirmed that the position of the Eocene-Oligocene boundary that most closely agrees with the charophyte distribution is that situated at the Middle Headon Beds.

THE Hampshire basin Palaeogene charophytes, which were described by Reid and Groves (1921), Groves (1926), and Grambast (1958), are of considerable stratigraphic importance, as the Hordle and the Bembridge floras form the basis of two charophyte zones (Castel 1968; Grambast 1972). The charophyte Verzenay (Hordle) Zone, which includes the mammal Euzet Zone (Feist-Castel 1971), is the highest presently defined in the Eocene. The Bembridge Zone, whose type-locality is the same age as Montmartre in the Paris basin (Stehlin 1909), corresponds to the Early Oligocene (Lattorfian) and to the base of the Middle Oligocene.

The Eocene-Oligocene boundary is taken as the base of the Middle Headon Beds, as suggested by Curry (1958). In order to establish the floristic evolution at the Eocene-Oligocene boundary, specimens were collected from the transitional series between the Lower Headon and Bembridge Beds in the Isle of Wight. Graduated samplings from the Middle and Upper Headon Beds, as well as from the Osborne Beds, proved to be very rich in specimens. The floras studied here came primarily from personal collecting. Samples found by Professor D. Curry were also studied.

LOCATION OF SAMPLES AND CHAROPHYTE DISTRIBUTION

The localities are well-documented cliff-sections on the western and eastern coasts of the Isle of Wight. Their position in the series is defined by the stratigraphic succession generally accepted since the work of Forbes (1856) and described in greater detail later (Bristow 1862; White 1921; Curry 1968).

Table 1 showing the sampling localities, is followed by a description of that part of the succession from which samples were taken, and which includes lists of charophyte species found.

TABLE 1. Distribution of charophyte localities in the Upper Eocene and Lower Oligocene succession of the Isle of Wight.

Localities Beds	Headon Hill	Cliff End	Horestone Point	Whitecliff Bay
BEMBRIDGE			●	● ●
OSBORNE		● ●		●
UPPER HEADON	● ●	●		
MIDDLE HEADON	●			
LOWER HEADON	●			

HEADON HILL (National Grid reference SZ 305 860)

(a) *Lower Headon Beds*. Only one sample was collected, 1 m above the white Barton sands.

Cream-coloured calcareous marls with shells (40 cm): *Psilochara polita*, *P. bistruncata* (scarce), *Stephanochara edwardsi*, *Grovesichara distorta*, *Harrisichara vasiformis*, *H. vasiformis-tuberculata*.

All these species occur within the Lower Headon Beds at Hordle, the flora of which was described by Reid and Groves (1921).

(b) *Middle Headon Beds*. Lower part; brackish clays with lignite ('*Neritina* beds'): *Gyrogonia wrighti*, *Grambastichara tornata*, *Chara antennata* (scarce).

The upper part, the marine 'Venus beds' and blue clays, did not yield any charophytes.

(c) *Upper Headon Beds*. Samples were collected from two stratigraphical positions in these beds:

(i) Approximately 3 m above the Middle Headon blue clays, cream-coloured marls with shells: *Gyrogonia wrighti*, *Harrisichara vasiformis-tuberculata*, *Grovesichara distorta*.

(ii) 3 m above the latter, cream-coloured calcareous clays with shells: *Gyrogonia wrighti*, *Sphaerochara subglobosa*, *Harrisichara vasiformis-tuberculata*.

In these Upper Headon Beds, Professor D. Curry collected charophyte gyrogonites which have been determined by the writer to be: *Gyrogonia wrighti*, *Grovesichara distorta*, *Chara antennata*, *Psilochara* sp., *Harrisichara* sp. (scarce).

CLIFF END (National Grid reference SZ 331 891)

(a) *Upper Headon Beds*. Cream-coloured marls lying above the Middle Headon Beds: *Grovesichara distorta*, *Harrisichara vasiformis-tuberculata*, *Psilochara* aff. *bitruncata*, *Sphaerochara subglobosa*.

This locality also revealed an insectivore mammal tooth, cf. *Spalacodon*, identified by Dr. B. Sigé.

(b) *Osborne Beds*. Samples were collected from two stratigraphical positions in these beds:

(i) About 30 m above the Upper Headon Beds, calcareous marls with ferruginous concretions: *Nitellopsis* (*Tectochara*) aff. *aemula*, *Harrisichara vasiformis-tuberculata*, *Psilochara* aff. *bitruncata*, *Sphaerochara subglobosa*.

With this flora was found a rodent tooth identified by Dr. M. Vianey-Liaud as *Theridomys* (*Theridomys*) *pseudosiderolithicus* De Bonis, -closely resembling that from La Debrugé.

(ii) Approximately 10 m above the ironstone band, multicoloured clays with concretions of argillaceous limestone: *Gyrogona wrighti*, *Harrisichara vasiformis-tuberculata*, *Psilochara* aff. *bitruncata*.

HORESTONE POINT (National Grid reference SZ 634 907)

Bembridge Limestone. About 1 m above the beach level: brown, then black, marls, topped by a limestone.

(i) Brown marls: *Harrisichara tuberculata*, *Nitellopsis* (*Tectochara*) *latispira*, *Gyrogona wrighti*, *Grovesichara distorta*, *Rhabdochara stockmansi* (scarce).

(ii) Black marls: *Harrisichara tuberculata*.

WHITECLIFF BAY (National Grid reference SZ 642 863)

(a) *Osborne Beds*. Yellow limestone with charophytes, topped by green marls containing: *Gyrogona wrighti*, *Harrisichara vasiformis-tuberculata*, *Sphaerochara* sp. (scarce), *Chara* sp.

(b) *Bembridge Limestone*—lower part.

(i) Pale-brown clayey limestone: *Harrisichara tuberculata*.

(ii) Superposed to the latter, black marls: *Harrisichara tuberculata*, *Sphaerochara subglobosa*.

Material found by Professor D. Curry in the Bembridge Limestone has been found to be: *Harrisichara tuberculata*, *Rhabdochara stockmansi*, *Gyrogona wrighti*, *G. caelata*.

SYSTEMATIC DESCRIPTIONS

Family CHARACEAE L. Cl. Richard, 1815

Genus GYROGONA Lamarck, 1904 ex Lamarck, 1822 emend. Grambast, 1956

Gyrogona wrighti (Salter ex Reid and Groves) Pia, 1927

1856 *Chara wrighti* Salter in Forbes, p. 160, pl. 7, figs. 15-21.

1921 *Chara wrighti* Salter ex Reid and Groves, p. 183, pl. 4, fig. 1.

- 1927 *Gyrogonites wrighti* Pia, p. 90.
- 1954 *Achistochara wrighti*, L. and N. Grambast, p. 59, fig. 1.
- 1954 *Brachychara wrighti*, L. and N. Grambast, p. 667.
- 1956 *Brevichara hordlensis* Horn af Rantzien, p. 245.
- 1957 *Gyrogona hordlensis*, Grambast, p. 280.
- 1958 *Gyrogona wrighti*, Grambast, p. 145.

Syntypes. Specimen nos. 74500, 76499, Geological Survey, London.

G. wrighti occurs in most of our localities (see Table 2). It is particularly abundant in the limestones, and in the brackish facies such as the Middle Headon *Neritina* Bed at Headon Hill. Gyrogonites from the same locality present quite notable morphological differences: the shape may be more or less subglobular (length/width ratio varying from 0.9 to 1.0), the spiral cells and apical nodules are faintly prominent, the size varying between broad limits (length 750–1100 μm , width 750–1125 μm). These differences, however, are within the limits of the species.

G. wrighti, known from the Bartonian (Calcaire de Saint-Ouen, Grambast 1972) to the Lower Oligocene, is of no stratigraphic use in this study.

Genus GROVESICHARA Horn af Rantzien, 1959

Grovesichara distorta (Reid and Groves) Horn af Rantzien

Plate 21, fig. 7

- 1921 *Chara distorta* Reid and Groves, p. 186, pl. 5, fig. 6.
- 1959 *Grovesichara distorta*, Horn af Rantzien, p. 125, pl. 15, figs. 1–7.
- 1959 *Grovesichara distorta*, Grambast, p. 8, fig. 2.

Lectotype. Reid and Groves 1921, pl. 5, fig. 6. Lowermost right-hand specimen (designated by Horn af Rantzien 1959). The type-material was found by Grambast (1958) to be at the British Museum and not in the collections of the Geological Survey.

This well-known species is easily recognizable by its massive and somewhat irregular shape and by its apex, where the thick and straightened cellular ends form a very convex cap. The basal plug is visible somewhat below the pore. Besides Hampshire, *G. distorta* has been reported from the Auversian and Bartonian by Grambast (1958, 1962) as well as from the Lower Oligocene by Riveline (1973). In the Isle of Wight, it occurs in the Upper and Lower Headon Beds, the latter being its type-stratum. Depending on the localities, variations occur in the length/width ratio of the gyrogonites. Thus, in the Lower Headon Beds at Headon Hill, this ratio is between 1.1 and 1.3, whereas in the Upper Headon Beds at Cliff End it is not far from 1.0, the general shape being more globular. The specimens gathered in the Upper Headon Beds at Headon Hill were not sufficiently abundant for population studies.

Genus NITELLOPSIS Hy, 1889

Sub-genus TECTOCHARA L. and N. Grambast, 1954

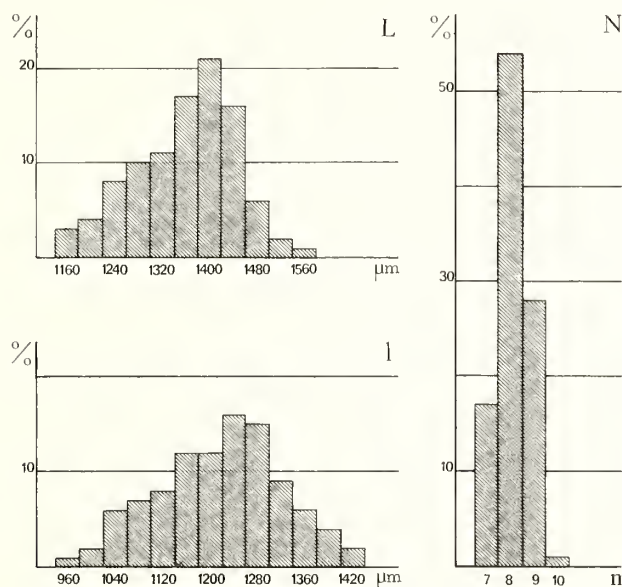
Nitellopsis (*Tectochara*) aff. *aemula* Grambast, 1972

Plate 22, fig. 4a–c

- 1972 *Tectochara meriani* L. and N. Grambast, 1954 ssp. *aemula* Grambast, p. 23, fig. 10, pl. 8, figs. 1–6.
- 1972 *Nitellopsis* (*Tectochara*) *aemula* (Grambast) Grambast and Soulié, p. 11.

Holotype. Specimen no. V 41 126, British Museum (Natural History), London.

This form occurs in the ironstone band of the Osborne Beds, at Cliff End. It is here considered as allied to *N. (T.) aemula* of the Lower Hamstead Beds, but it is not impossible that it might be hereafter attributed to a new and distinct species. Characters common to both are the ovoid shape with a thin basal region, the similar dimensions, and the basal pore of small diameter. The form from Cliff End differs from *N. (T.) aemula* by its somewhat longer general shape, the less prominent base, the less marked basal funnel, and the basal plug which is relatively thick for a *Tectochara*.



TEXT-FIG. 1. *Nitellopsis (Tectochara) latispira* n. sp. Histograms showing the variation in gyrogonite length (L), width (l), and number of convolutions (N). One hundred specimens measured.

Nitellopsis (Tectochara) latispira n. sp.

Plate 22, fig. 3a-d

Holotype. Specimen no. C.F. 1584-1; Université des Sciences et Techniques, Montpellier, France.

Paratypes. Specimen nos. C.F. 1584-2 to 1584-5; Université des Sciences et Techniques, Montpellier, France.

Type-locality and horizon. Horestone Point, Isle of Wight (SZ 634 907); brown marls at the base of Bembridge Limestone.

Material. About 500 specimens.

Diagnosis. Gyrogonite subglobular to ovoid, apex truncated or slightly convex, basal region thin, protruding, and truncated. Cells somewhat thinner and narrower at periphery of apex; apical ends of cells gradually widening, usually with only slightly prominent nodules. Basal ends entirely calcified and delimiting a wide basal funnel. Pore small, measuring 50–80 μm ; relatively thick plug of 170–280 μm in diameter and 130–180 μm in thickness.

Dimensions. 1160–1560 μm , often 1360–1440 μm long; 960–1420 μm , often 1140–1280 μm wide; length/width ratio: 0.98–1.30; 7–10 convolutions. Cells smooth, flat to slightly convex, 160–260 μm high.

Affinity. This new species agrees with the genus *Nitellopsis* in the general shape of its gyrogonites, more often higher than wide, in the shape of the periapical region where the cells become thinner and narrower, and in the apical nodules which, however, are not very prominent. The thin base and well-developed basal funnel are characteristic of the subgenus *Tectochara*. Among the known species, the subglobular shape and narrow base of *N. (T.) latispira* recalls *N. (T.) supraplana* (Peck and Recker) Grambast and Soulié from the Eocene of Peru, but differs by its greater dimensions, especially in length. The shape and the base of this new species is also suggestive of *N. (T.) aemula* (Grambast) Grambast and Soulié, from the Lower Hamstead Beds of Isle of Wight, but differs by the less protruding base, which in the latter is emphasized by depressions in front of the basal ends of the cells. The gyrogonite is also more globular in *N. (T.) latispira*, the cell width and height of the plug are greater, and there is one less convolution of the spiral cells.

Genus SPHAEROCHARA Mädlar, 1952 emend. Horn af Rantzien and Grambast, 1962
Sphaerochara subglobosa (Groves) Horn af Rantzien, 1959

Plate 21, figs. 8, 9

1926 *Chara subglobosa* Groves, p. 172, pl. 12, fig. 3.

1959 *Sphaerochara subglobosa*, Horn af Rantzien, p. 129.

Syntype. Specimen no. V. 18331, British Museum (Natural History), London.

Identification. Grove's species had not, until now, been rediscovered, or perhaps not recognized, because of the inadequacy of the original illustration. Despite Grove's very complete diagnosis, only a thorough examination of the type-material allowed us to ascribe to this species some *Sphaerochara* from the Isle of Wight, as well as some other specimens previously collected in the Lower Oligocene of the south of France.

Description. Gyrogonite subglobular to broadly ellipsoid; apex convex, base truncated. Spiral cells with granulose surface, ornamented with massive nodules, as high as the cells, generally laterally elongated, disappearing at the periphery of the apex. Apical ends of the cells bulging, forming a rosette where the thickness of the

EXPLANATION OF PLATE 21

Fig. 1. *Harrisichara vasiformis* (Reid and Groves) Grambast, lateral view, $\times 60$; from Lower Headon Beds, Headon Hill.

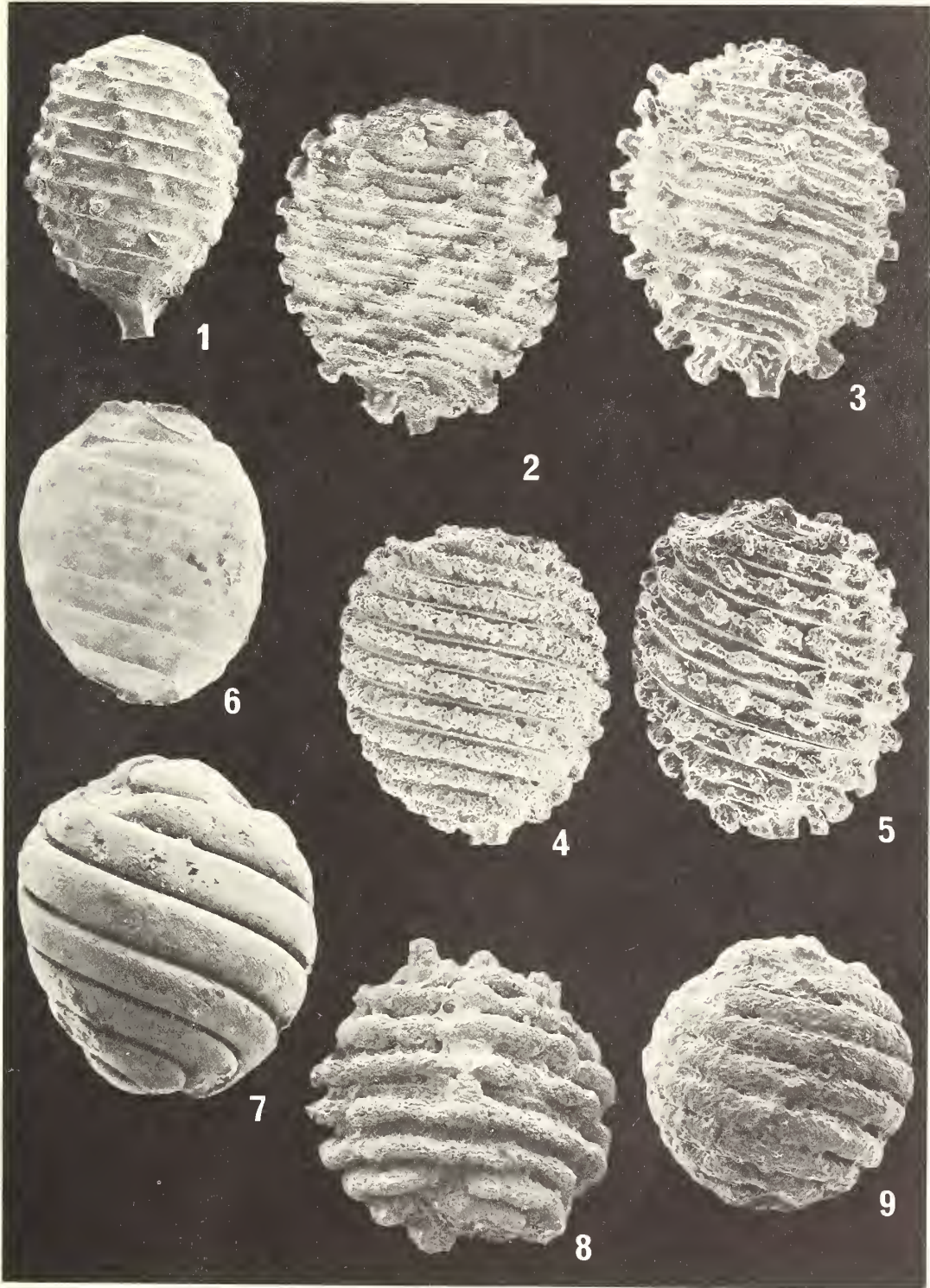
Figs. 2–3. *Harrisichara vasiformis-tuberculata*, lateral view, $\times 60$; from Upper Headon Beds; 2, from Headon Hill; 3, from Cliff End.

Figs. 4–5. *Harrisichara tuberculata* (Lyell) Grambast, lateral view, $\times 50$; from Bembridge Beds; 4, from Horestone Point; 5, neotype, from Whitecliff Bay.

Fig. 6. *Psilochara* aff. *conspicua* Grambast, lateral view, $\times 50$; from Upper Headon Beds, Cliff End.

Fig. 7. *Grovesichara distorta* (Reid and Groves) Horn af Rantzien, lateral view, $\times 45$; from Lower Headon Beds, Headon Hill.

Figs. 8–9. *Sphaerochara subglobosa* (Groves) Horn af Rantzien, lateral views, $\times 90$; 8, from Upper Headon Beds, Cliff End; 9, from Osborne Beds, Whitecliff Bay.



FEIST-CASTEL, Charophytes from the Isle of Wight

cells increases again, thus forming nodules similar to the lateral ones; apical nodules sometimes undeveloped. Basal plug level with the pore, surrounded by a crown of nodules.

Dimensions. 350–500 μm long, 350–475 μm broad, spiral cells 50–65 μm wide, showing 6–9 convolutions.

Relationships. This species clearly corresponds with the genus *Sphaerochara* in its general globose shape, its small size, the prominent apical rosette, and the basal plug level with the pore. It differs from other known species of the genus in its ornamentation.

Stratigraphic significance. In the Isle of Wight, *S. subglobosa* occurs in several localities in the Upper Headon, Osborne, and Bembridge Beds. According to Groves, it persists into the Lower Hamstead Beds; it does not seem to occur below the Upper Headon Beds. *S. subglobosa* is thus the only species which makes its appearance between the Lower Headon and Bembridge Beds, other taxa present being persistent Eocene or intermediate Eocene–Oligocene forms.

Genus HARRISICHARA Grambast, 1957

Harrisichara vasiformis (Reid and Groves) Grambast, 1957

Plate 21, fig. 1

1921 *Chara vasiformis* Reid and Groves, p. 185, pl. 4, figs. 12–15.

1927 *Kosmogyrva vasiformis*, Pia, p. 90.

1957 *Harrisichara vasiformis*, Grambast, p. 347, pl. 6, fig. 4.

Lectotype. Specimen no. 76528, Geological Survey, London. Designated and refigured by Grambast (1957).

The Lower Headon Beds (Upper Bartonian) are characterized by typical specimens of *H. vasiformis* recognizable by their narrow base and rounded apex. The same typical aspect is shown by populations of *H. vasiformis* in beds of the same age in the south of France, in the Alès basin for example (Feist-Castel 1971). However, at Headon Hill and at the type-locality at Hordle (Hampshire mainland) specimens are found of similar size but which have a more rounded base and more flattened apex, a shape which is suggestive of *H. tuberculata*.

Harrisichara tuberculata (Lyell) Grambast, 1957

Plate 21, figs. 4, 5

1826 *Chara tuberculata* Lyell, p. 94, pl. 13, figs. 7, 8.

1828 *Chara tuberculosa*, Ad. Brongniart, p. 72.

1850 *Chara tuberculosa*, Unger, p. 33.

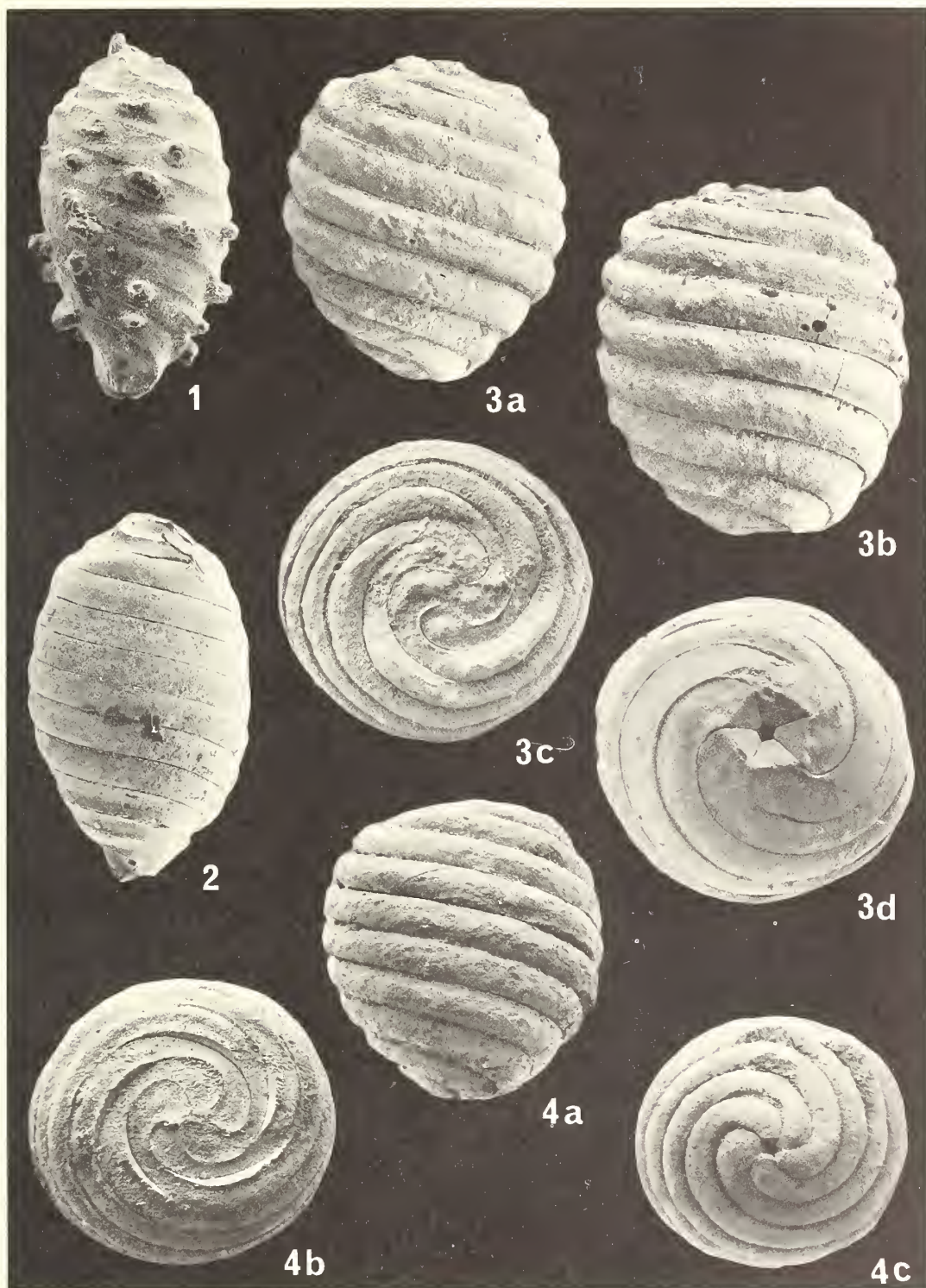
EXPLANATION OF PLATE 22

Fig. 1. *Chara antennata* Grambast, lateral view, $\times 110$; from Upper Headon Beds, Headon Hill.

Fig. 2. *Grambastichara tornata* (Reid and Groves) Horn af Rantzien, lateral view, $\times 70$; from Middle Headon Beds, Headon Hill.

Fig. 3. *Nitellopsis* (*Tectochara*) *latispira* n. sp., $\times 35$; 3a, paratype, lateral view; 3b, holotype, lateral view; 3c, paratype, apical view; 3d, paratype, basal view.

Fig. 4. *Nitellopsis* (*Tectochara*) aff. *aemula* Grambast, $\times 35$; 4a, lateral view; 4b, apical view; 4c, basal view; from Osborne Beds, Cliff End.



FEIST-CASTEL, Charophytes from the Isle of Wight

- 1920 *Chara archiaci* Watelet var. *tuberculata*, Dollfus and Fritel, p. 252.
 1927 *Kosmogrya tuberculata*, Pia, p. 90.
 1957 *Harrisichara tuberculata*, Grambast, pl. 6, figs. 1-3, 8-10.

Neotype (the type-material has not been located). Specimen no. C.F. 1585b-1, Université des Sciences et Techniques, Montpellier, France. It is figured here (Pl. 21, fig. 5).

Locality. Whitecliff Bay, Isle of Wight; marls in lower part of Bembridge Limestone.

H. tuberculata is abundant from the base of the Bembridge Beds upwards (Horestone Point, Whitecliff Bay) and extends into the Lower Hamstead Beds. It is a sure indicator of the Lower (but not lowermost) Oligocene and of the base of the Middle Oligocene.

Morphologically it is characterized by its broad ellipsoidal shape, its well-defined but short basal stalk, and by its dimensions. The variability of the ornamentation is another feature of the species; the tubercles are either connected by a thin median line, or merged into a nodular ridge which may or may not extend to the apex. More rarely, isolated tubercles, separated from one another by one or two smaller tubercles, may be observed.

Harrisichara vasiformis-tuberculata

Plate 21, figs. 2, 3

Harrisichara vasiformis and *H. tuberculata* are two distinct and easily recognizable species. However, in Hampshire, from the Lower Headon Beds upwards and mainly in the series occurring between these and the Bembridge Beds, specimens of *Harrisichara* are found which are morphologically intermediate between these two species.

Table 2 summarizes the features peculiar to each population.

The forms intermediate between *H. vasiformis* and *H. tuberculata* are not restricted to Hampshire; they are also found in the Lowermost Oligocene in southern France (Triat and Truc 1972; Feist-Castel 1975). Due to their wide geographical distribution and short vertical extension, they are of real stratigraphic value.

Genus *PSILOCHARA* Grambast, 1959

Psilochara bitruncata (Reid and Groves) Feist-Castel, 1971

- 1921 *Chara strobilocarpa* var. *bitruncata* Reid and Groves, p. 188, pl. 5, fig. 13.
 1959 *Charites bitruncata*, Horn af Rantzien, p. 67, pl. 3, figs. 1-4.
 1971 *Psilochara bitruncata*, Feist-Castel, p. 166.

Lectotype. Specimen no. V 24122, British Museum (Natural History), London, designated here from the type material figured by Reid and Groves (1921).

Description. Gyrogonite elongated, apex truncated, base narrowed. Spiral cells concave to flat, smooth. Apical ends of the cells pointing upwards; junction line very short.

Dimensions. 800-900 μm long, 660-760 μm broad. Spiral cells 110-120 μm wide, showing 7-8 convolutions.

Distribution. *P. bitruncata*, whose type-locality is at Hordle, occurs infrequently in the Lower Headon Beds at Headon Hill. Besides Hampshire, it has been reported from the Upper Bartonian of southern France.

TABLE 2. Comparison of *Harrisichara* from the Lower Headon to Hamstead Beds, Isle of Wight.

	<i>H. vasiformis</i>	<i>H. vasif.-tubercul.</i>	<i>H. tuberculata</i>
General shape	long, ovoid tapering base	ovoid to ellipsoid	wide ellipsoid
Dimensions			
lengths	720-950 μm	680-920 μm	820-1160 μm
widths	500-760 μm	600-760 μm	760-1000 μm
cell widths	60-100 μm	50-90 μm	100-125 μm
Ornamentation	often isolated tubercles, separated by smaller ones	tubercles often connected by a median line	tubercles connected by a median line or merged, forming a nodular ridge
Stratigraphic distribution	Lower Headon Beds	Lower & Upper, Headon Beds, Osborne Beds	Bembridge & Hamstead Beds

Closely related forms. In the Upper Headon Beds at Headon Hill and Cliff End, as well as in the Osborne Beds at Cliff End, *Psilochara* is very abundant and appears to be similar to *P. bitruncata*, without being definitely assignable to it. In these populations, three different forms are distinguishable:

1. Specimens similar to *P. bitruncata* in having an elongated shape, usually with concave cells but with their dimensions slightly greater.
2. Specimens of the same shape and dimensions as the former, but with convex cells (Pl. 21, fig. 6) recalling *P. conspicua* Grambast.
3. Specimens of ovoid shape, with flat or convex (rarely concave) cells, also characterized by a clear apical zone of large diameter (480-580 μm) and by wavy sutures in the lower region of the gyrogonites. Apart from its longer shape, this form is very similar to *P. repanda* Grambast.

Psilochara polita (Reid and Groves) Grambast, 1959

- 1921 *Chara polita* Reid and Groves, p. 187, pl. 5, figs. 9, 12.
 1927 *Gyrogonites politus*, Pia, p. 90.
 1959 *Peckichara polita*, Horn af Rantzien, p. 116, pl. 13, figs. 1-3.
 1959 *Psilochara polita*, Grambast, p. 11.

Lectotype. Reid and Groves 1921, pl. 5, fig. 12; designated by Grambast 1958, p. 179. Slide 76521, Geological Survey, London.

P. polita, which is associated with *P. bitruncata* in the Lower Headon Beds at

Headon Hill, differs from the latter by its ovoid shape, its dimensions ($680\text{--}880\text{ }\mu\text{m} \times 600\text{--}720\text{ }\mu\text{m}$), the number of convolutions (8–10), and the undulations of the sutures.

Genus STEPHANOCHARA Grambast, 1959
Stephanochara edwardsi Grambast, 1958, p. 168

Holotype. Specimen no. 9-6-19, British Museum (Natural History), London.

This species is abundant in the Lower Headon Beds at Headon Hill, but was not found in younger beds. From a morphological point of view, *S. edwardsi* is very close to *S. grambasti* Feist-Castel, a species of nearly the same age from southern France. The latter is, however, easily distinguishable by its narrower basal region and the less well-marked, or even non-existent, periapical constrictions.

Genus RHABDOCHARA Mädlar, 1955 emend. Grambast, 1962
Rhabdochara stockmansii Grambast, 1957

Holotype. Specimen no. C. 140-1, Grambast Collection, Université des Sciences et Techniques, Montpellier, France.

R. stockmansii occurs infrequently in the Bembridge Beds at Horestone Point and at Whitecliff Bay. This species, which extends into the Lower Hamstead Beds, is common in other regions of Europe particularly at the base of the Middle Oligocene (e.g. Hoogbutsel, Belgium; Ronzon, France).

Genus GRAMBASTICHARA Horn af Rantzien, 1959
Grambastichara tornata (Reid and Groves) Horn af Rantzien, 1959

Plate 22, fig. 2

- 1921 *Chara tornata* Reid and Groves, p. 187, pl. 5, figs. 1–3.
- 1927 *Gyrogonites tornatus*, Pia, p. 90.
 non Tectochara tornata, Mädlar, 1955, p. 296, taf. 26, figs. 19–22.
- 1959 *Grambastichara tornata*, Horn af Rantzien, p. 70, pl. 4, figs. 1–6.

Holotype. None designated.

Lectotype. Reid and Groves 1921, pl. 5, fig. 3 (designation by Mädlar 1955). Specimen no. 16519, Geological Survey, London.

Although the type-locality is the equivalent of that at Hordle, *C. tornata* was not found in the Lower Headon Beds of the Isle of Wight (from which I collected only very little material). This species is abundant in the Middle Headon *Neritina* Beds, at Headon Hill. The specimens are very similar to those described by Reid and Groves; only the dimensions are slightly different, the upper and lower limits of variation of length and width being $100\text{ }\mu\text{m}$ greater.

In both localities, the apical rosette which characterizes the genus of Horn af Rantzien is not in every case obvious in *G. tornata*, its type-species. On the contrary, nearly half of the specimens present a pattern quite similar to that of *Chara*. It differs from *Chara* only in the cellular relief, concave in the latter, convex or flat in *G. tornata*. It is thus obvious that the separation of *Grambastichara* from *Chara* remains problematical, a question already raised by Grambast (1962).

Chara antennata Grambast, 1958

Plate 22, fig. 1

1958 *Chara antennata*, Grambast, p. 188.

Holotype. Specimen no. C. 244-6, Grambast Collection, Université des Sciences et Techniques, Montpellier, France.

Description. General shape cylindrical, apex convex, base tapering. Spiral cells flat to slightly concave, ornamented with very prominent cylindrical tubercles. Apical ends of the cells concave. Basal pore pentagonal, without a peripheric funnel.

Dimensions. 450–620 μm long, 350–400 μm wide, 8–11 convolutions.

Distribution. In the Isle of Wight, *C. antennata* occurs in the Upper Headon Beds and, very rarely, in the Middle Headon Beds. Besides these localities, it has been reported from 'Marnes à Pholadomyes' (Upper Bartonian) of the Paris basin by Grambast (1958) and Riveline (1973), and also from a locality of the Alès basin by the author (1971).

STRATIGRAPHIC IMPLICATIONS OF THE CHAROPHYTE DISTRIBUTION

In Table 3, the above data are added to those from Reid and Groves (1921), Groves (1926), and Grambast (1958, summarized by Curry 1966), concerning the floras of the Lower Headon (Hordle), Bembridge, and Hamstead Beds.

This study revealed the floras, which were previously unknown, in the levels between the Lower Headon and the Bembridge Beds. From the established succession, one can see that the change in the floras from the Verzenay (Hordle) Zone to the Bembridge Zone is progressive, whereas the transition previously appeared to be more abrupt.

Concerning the position of the presently controversial Eocene–Oligocene boundary, charophytes provide no decisive information, since the stratigraphic divisions are essentially based upon marine faunas. We have, therefore, indicated only the divisions which seem most consistent with their distribution.

In the Palaeogene of the Isle of Wight and of Hampshire in general, the most obvious floristic changes occur at two levels. First, in the Upper Headon Beds where, after the disappearance of numerous species from the Lower Headon Beds, there appears *Sphaerochara subglobosa* which extends into the Lower Hamstead Beds. Although the floras of the Lower and Upper Headon Beds remain quite distinct (those of the Middle Headon Beds being of no stratigraphic value), it cannot be called a real renewal, since several Bartonian species extend into the Upper Headon Beds, and since transitional forms are observed there as well. The second change occurs at the level of the Bembridge Beds, where there appears typical *H. tuberculata* as well as the genus *Rhabdochara*, represented by *R. stockmansii*. Here the break appears more distinct than previously; however, in other regions (notably the south of France), the transitional flora, which in the Isle of Wight figures only in the Upper Headon and Osborne Beds, may extend into levels equivalent to the Bembridge Beds (work on this subject is now in progress). It is thus noted that the distribution of the charophytes would not usually lend itself to a break at this level. Likewise, the floristic composition does not vary noticeably between the Bembridge and Lower

TABLE 3. Vertical extension of Charophyte floras in the Upper Eocene and Lower Oligocene of Hampshire.

EOCENE		OLIGOCENE		Age	
Verzenay		Bembridge		Charophyte zones	
				Beds	
				Species	
LOWER HEADON	MIDDLE HEADON	UPPER HEADON	OSBORNE	BEMBRIDGE	LOWER HAMSTEAD

Hamstead Beds; although they may be distinguished by the presence of characteristic species, these two levels do in fact have a number of species in common: *H. tuberculata*, *R. stockmansii*, *S. subglobosa*, and *G. wrighti*.

The position of the Eocene-Oligocene boundary which best agrees with the charophyte distribution is thus the one presently accepted by the Stratigraphical Lexicon (Denizot 1957; Curry 1958).

Acknowledgements. The material found by Professor D. Curry (University College, London) was sent by him to Professor L. Grambast (Université de Montpellier-2) who loaned it for the present study. I wish to express my thanks to both. I am also indebted to Dr. G. F. Elliott and Mr. C. H. Shute (Palaeontology Department, British Museum (Natural History)), for permitting me to examine specimens from the Groves Collection.

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CLASSIFICATION AND PHYLOGENY OF HOMALONOTID TRILOBITES

by A. T. THOMAS

ABSTRACT. The composition, classification, and phylogeny of the Homalonotidae are discussed, and new family and subfamily diagnoses given. *Plaesiacomia hughesi* sp. nov. and *P. vacuvertis* sp. nov. from the Llanvirn of Wales and Saudi Arabia respectively, and *Platycoryphe dyaulax* sp. nov. from the Llandovery of Saudi Arabia, are described.

SOME of the problems involved in classifying homalonotid trilobites have arisen because the Silurian and Devonian genera are known principally from old, inadequate descriptions. The difficulties are increased by the rarity of Ashgill and Llandovery forms which has emphasized the apparent morphological gap between post-Ordovician and older genera. Study of the species described here, together with work on middle and upper Silurian homalonotines to be published elsewhere, has shed new light on the classification and phylogeny of the family.

Repositories. The following abbreviations are used herein: BM—British Museum (Natural History), London; GSM—The Geological Museum, Institute of Geological Sciences, London; SM—Sedgwick Museum, Cambridge.

SYSTEMATIC PALAEOLOGY

Family HOMALONOTIDAE Chapman, 1890
[= Portaginidae Lespérance, 1968]

Diagnosis. The following diagnosis is based on that of Szdzy (in Moore 1959, pp. 0454–0455) and incorporates the correction and emendation noted by Whittington (1965, p. 488).

Cephalic border rarely well defined, often absent. Glabella narrowing forwards, with four or fewer pairs of lateral glabellar furrows. Paraglabellar area usually present. Genal angle generally rounded with facial suture displaying gonatoparian condition; opisthoparian or proparian sutures and genal spine rarely occur. Palpebral lobe small, eye ridge present in some early forms. Rostral plate narrows posteriorly. Rostral suture ventral or marginal in early genera, dorsal in later forms. Hypostome subquadrate, with small anterior wing and weakly developed lateral notch; posterior margin rarely rounded, usually bifurcate. Thorax of thirteen segments; axis moderately wide in early genera, indistinct and very broad in later ones. Pleural tips blunt. Pygidium subsemicircular to triangular in outline.

Discussion. *Brongniartella* Reed, 1918; *Burmeisterella* Reed, 1918; *Burmeisteria* Salter, 1865; *Calymenella* Bergeron, 1890; *Colpocoryphe* Novák in Perner 1918;

Digonus Gürich, 1909; *Dipleura* Green, 1832; *Eohomalonotus* Reed, 1918; *Parahomalonotus* Reed, 1918; *Plaesiacomia* Hawle and Corda, 1847; and *Trimerus* Green, 1832 are sufficiently well known for no doubt to arise concerning their membership of the family.

Henningsmoen (*in* Moore 1959, p. 0524) regarded *Platycoryphe* Foerste, 1919 as of uncertain affinities but I agree with Whittington (1965) that it is a homalonotid. Přibyl (1953, p. 16) placed *Bavarilla* Barrande, 1868 in the Olenidae but it was excluded therefrom by Henningsmoen (1957, p. 20). *Bavarilla* is accepted as a homalonotid and its systematic position is discussed further below. No good illustrations are available of *Leiostegina* Kobayashi, 1937 but the anteriorly narrowing glabella and transversely straight, apparently dorsal, rostral suture (see Kobayashi 1937, pl. 6, fig. 18) suggest that it is a homalonotid. Professor S. Kuss (Paläontologisches Institut, Freiburg) informed me (*pers. comm.*, 8 October 1975) that the type material of *L. inexpectans*, the only known species, seems to be lost. A more detailed appraisal of *Leiostegina* must therefore await the availability of topotype material.

The available illustrations of *Pamirotellus* Balashova, 1968 (= *Pamirites* Balashova, 1966; *non* Toumansky, 1938) are poor but what can be seen suggests that it is a synonym of *Brongniartella*. In particular, the pygidium is longer than wide, well segmented, and obtusely pointed posteriorly (Balashova 1966, pl. 2, fig. 6; 1968, pl. 52, fig. 5c). The glabella (Balashova 1966, pl. 2, fig. 7; 1968, pl. 52, fig. 5d) is constricted (*tr.*) anteriorly, a feature typical of many *Brongniartella* species. Balashova gives the horizon of *Pamirotellus* as Wenlock whereas *Brongniartella* is not known elsewhere after the lower Llandovery. Possibly a relic species is represented or the horizon given may be incorrect. Since no other faunal elements are listed from this horizon the reasons for suggesting a Wenlock age are unclear. *Portaginus* Lespérance, 1968, from the upper Ashgill of Quebec, is also synonymous with *Brongniartella* (see Dean 1976, pp. 238–239). *Liangshianaspis* Chang, 1974 shows no major differences from *Platycoryphe*. Apollonov (1974, pp. 59–61, pl. 11, figs. 1–11; pl. 12, figs. 1–6, 8) recently redescribed the type species, and referred it to that genus.

Neseuretus Hicks, 1873 (see Whittard 1960, p. 139 for use of this name rather than *Synhomalonotus* Novák *in* Perner 1918) has been regarded as a homalonotid by various authors but I agree with Whittington (1966a, pp. 499–500) that it is a calymenid. *Lakaspis* Kobayashi, 1937 was provisionally assigned to the Homalonotidae by both Kobayashi and Hupé (1953). The available illustrations (Kobayashi 1937, pl. 2, figs. 27, 28; Lake 1906, pl. 11, figs. 2, 3) are poor but it is clear that the glabella expands (*tr.*) in its anterior half. This indicates that *Lakaspis* is not a homalonotid and Jaanusson (*in* Moore 1959, p. 0358) questionably assigned it to the Nileidae. Clarke (1913) erected *Homalonotus* (*Schizopyge*) *parana* for a pygidium from the lower Devonian of Brazil. The specimen displays no homalonotid features and Struve (1958) erected the calmonioid genus *Tibagya* to receive it (see also Struve *in* Moore 1959, p. 0486).

Classification of the Homalonotidae. Hupé (1953, 1955) placed the Homalonotidae in the superfamily Calymenoidea (which he attributed to Swinnerton 1915). He

proposed three subfamilies based on cephalic and pygidial shape, form of the rostral suture, and distinctness of trilobation:

EOHOMALONOTINAE	<i>Eohomalonotus</i> , <i>Calymenella</i> , <i>Plaesiacomia</i>
HOMALONOTINAE	<i>Homalonotus</i> , <i>Burmeisterella</i> , <i>Brongniartella</i> , <i>Parahomalonotus</i> , <i>Digonus</i> , ? <i>Lakaspis</i> , ? <i>Leiostegina</i>
TRIMERINAE	<i>Trimerus</i> , <i>Burmeisteria</i> , <i>Dipleura</i>

Hupé (1953, p. 232) included *Neseuretus* in the Calymenidae but in 1955 erected the calymenid subfamily Colpocoryphinae to include *Neseuretus*, *Colpocoryphe*, and the non-papillate calymenids.

In Sdzuy's (1957; in Moore 1959, pp. 0454–0461) revision, *Bavarilla* was accepted as a homalonotid and placed in its own subfamily. Sdzuy's other subfamilies are as follows:

EOHOMALONOTINAE	<i>Calymenella</i> (<i>Calymenella</i>), <i>C.</i> (<i>Eohomalonotus</i>), <i>Brongniartella</i> , <i>Neseuretus</i> (this was simultaneously classified as a calymenid, p. 0453; and listed as <i>incertae sedis</i> , p. 0523)
COLPOCORYPHINAE	<i>Colpocoryphe</i> , <i>Plaesiacomia</i> , ? <i>Leiostegina</i>
HOMALONOTINAE	<i>Homalonotus</i> , <i>Burmeisterella</i> , <i>Burmeisteria</i> (<i>Burmeisteria</i>), <i>B.</i> (<i>Digonus</i>), <i>Parahomalonotus</i> , <i>Trimerus</i> (<i>Trimerus</i>), <i>T.</i> (<i>Dipleura</i>)

Hupé's Trimerinae was not recognized. Přibyl (1957, p. 92) had pointed to the close similarities between trimerines and homalonotines—especially the tendency to ill-defined trilobation, broad thoracic axis, and similar length to breadth proportions of the cephalon and pygidium.

Kobayashi (1960) erected the Synhomalonotinae to include *Neseuretus* and the calymenid *Vietnamia*. Having accepted Whittard's (1960) arguments for regarding *Synhomalonotus* as a junior synonym of *Neseuretus*, Kobayashi (1969, p. 243) proposed 'Neseuretinae' as a replacement subfamily name. This procedure contravenes Article 40 of the ICZN and 'Synhomalonotinae' must be retained. As *Neseuretus* is regarded as a calymenid, this subfamily is referred to the Calymenidae (see also Whittington 1971).

Subsequent workers have viewed the suprageneric classification of calymenaceans in different ways. Some authors (Dean 1966a; Hughes 1969; Henry 1971; Sadler 1974) favour several different families, others (Whittington 1966a, 1971; Dean 1971) utilize a number of different subfamilies assigned to either the Calymenidae or Homalonotidae.

A number of genera are present in the Tremadoc and Arenig from which younger calymenids and homalonotids arose (see Whittington 1966a, p. 500). While accepting that such early genera may not be easily accommodated in either group, I consider that the familial classification should reflect this essentially bipartite pattern. Within the Homalonotidae, three subfamilies are recognized for post-Tremadoc forms. The Cambrian ancestors of homalonotids are unknown but *Bavarilla* seems to be related. Hence the Bavarillinae Sdzuy, 1957 (as diagnosed by Sdzuy in Moore 1959, p. 0455) is retained.

Subfamily EOHOMALONOTINAE Hupé, 1953

Diagnosis. Cephalon subtriangular, rounded anteriorly; with anteriorly widened border. Glabella trapezoidal to parabolic; three or fewer pairs of lateral glabellar furrows, 1p sigmoidal. Paraglabellar area defined. Rostral suture is marginal or nearly so and describes a wide, forwardly convex curve. Facial suture gonatoparian. Thorax with distinct, moderately wide axis. Pygidium triangular, wider than long, with distinct trilobation.

Genera. *Eohomalonotus*, *Calymenella*.

Remarks. Reed (1918, p. 321) erected *Eohomalonotus* (*pro Brongniartia* Salter, 1865 (*pars*); *non* Leach, 1824, *nec* Eaton, 1832) as one of his subgenera of *Homalonotus*. Reed included a number of forms now referable to *Platycoryphe* as well as species of *Eohomalonotus* as presently understood, and distinguished it from *Calymenella* by the lack of a projecting frontal area. Sdzuy (*in* Moore 1959, pp. 0455-0456) regarded *Eohomalonotus* as a subgenus of *Calymenella*, the two being distinguished by the position of the rostral suture and degree of development of pygidial interpleural furrows, as well as the structure of the frontal area. Little recent information is available and whether two distinct genera are represented is a matter which must await further research.

Many authors have placed *Platycoryphe* and *Brongniartella* in the Eohomalonotinae. I regard them as homalonotines and reasons for doing so are given in the discussion of that subfamily.

Subfamily COLPOCORYPHINAE Hupé, 1955

Diagnosis. Cephalon subcircular; convex (tr. and sag.), sometimes highly so. Frontal area short (sag.), no anterior or lateral border. Rostral suture marginal. Glabella clearly defined. Palpebral lobe anteriorly placed. Cheek strongly declined laterally; genal angle well rounded, facial suture gonatoparian. Thoracic axis well defined. Pygidial axis wide and well defined. Border furrow deep; border flexed strongly downwards.

Genera. *Colpocoryphe*, *Plaesiacomia*.

Remarks. Vaněk (1965), like Hupé (1955) and Dean (1971), excluded the Colpocoryphinae from the Homalonotidae and considered them to be calymenids close to *Neseuretus*. The cephalic and glabellar shape, presence of paraglabellar areas (in many species), lack of anterior and lateral cephalic border, marginal rostral suture, moderately wide thoracic axis, thoracic structure, and the poorly segmented pygidium (which lacks interpleural furrows) suggest that colpocoryphines are homalonotids.

Sdzuy (*in* Moore 1959) questionably assigned *Leiostegina* to this subfamily. The genus is poorly known but shows no obvious features suggestive of a colpocoryphine relationship and I regard it as of uncertain subfamilial position.

Genus *PLAESIACOMIA* Hawle and Corda, 1847

Type species. *P. rara* Hawle and Corda, 1847, p. 55, pl. 3, fig. 30; from the Caradoc of Bohemia; by monotypy.

Other species. *P. hughesi* sp. nov.; *P. oehlerti* (Kerforne, 1900); *P. vacuvertis* sp. nov.; ?*P. brevicaudata* (Deslongchamps, 1825).

Diagnosis. Colpocoryphine with weakly impressed lateral glabellar furrows, glabella tapering rapidly forwards. Paraglabellar areas usually present; eye ridges absent. Pygidial axis with up to four (?five) weakly defined rings.

Discussion. Vaněk's (1965) view that *Colpocoryphe* and *Plaesiacomia* were synonymous was questioned by Dean (1966b, pp. 140–141) who listed nine distinguishing characters. Five of these—cephalic convexity, depth of anterior arch, and height of the pygidial axis (all greater in *Colpocoryphe*), position of pygidial border furrows, and degree of divergence of the pygidial margins—are interdependent characters connected with enrolment (see Clarkson and Henry 1973). Two more, the development of glabellar furrows and eye ridges, are too variable to be reliable discriminatory characters. Glabellar furrows are usually strongly developed in *Colpocoryphe*, but in a few cases are as weak as in *Plaesiacomia* (see Whittington 1953). Paraglabellar areas occur in all *Plaesiacomia* species known to Dean, but are absent in *P. hughesi*. Two of the features listed by Dean can be reliably used to distinguish between the genera: the glabella in *Colpocoryphe* species is bell-shaped, slightly tapering, with an inflated frontal lobe, while that of *Plaesiacomia* tapers more rapidly to a low frontal lobe and the pygidial axis lacks the clear segmentation of *Colpocoryphe*. *Colpocoryphe* species are poorly known and a revision is necessary before a decision concerning its status can be reached.

Plaesiacomia hughesi sp. nov.

Plate 23, figs. 1–5, 7

- v. 1969 *Plaesiacomia* sp.; Hughes, pp. 95–96, pl. 13, figs. 4–8; pl. 14, figs. 1–2.
. 1972 *Plaesiacomia* sp.; Robardet *et al.*, p. 122.

Name. After Dr. C. P. Hughes, who first described this species and made additional material available for study.

Holotype. BM It3024, incomplete internal mould of cranium, from Ordovician, lower Llanvirn, exposure on the left bank in the ravine in the upper reaches of Camnant Brook immediately north of the S bend 230 yd (207 m) S. 13° W. of the fence crossing the stream source, Builth district, Powys (Radnorshire) (SO 088 575).

Paratypes. BM It13815ab, incomplete cephalon; It13816–13819, It13821ab, It13823ab, cranidia; It3025, external mould of cranium; It13822ab, It13824ab, It13825ab, It13826–13827, It3023, It3026ab–3027, pygidia; It13820, external mould of pygidium.

Diagnosis. *Plaesiacomia* species with palpebral lobe placed two-thirds the way along the cephalon from the posterior margin. Glabellar furrows absent or very weak; paraglabellar areas absent. Pygidial axis with four (?five) ring furrows on the internal mould.

Description. The following points supplement the description given by Hughes (1969, pp. 95–96). Three pairs of very faint glabellar furrows are developed in the holotype

(Pl. 23, fig. 3a–b), but these are not clearly seen in other specimens. The pygidial border is broad, almost vertically inclined, and narrows somewhat beneath the posterior tip of the axis.

Discussion. Hughes (1969, p. 96) referred this species to *Plaesiacomia* because of the glabellar outline, poor development of lateral glabellar furrows, lack of prominent eye ridges, and shallow anterior arch. I accept this assignation but in the lack of paraglabellar areas, *P. hughesi* is reminiscent of *Colpocoryphe* species. The pygidial axis has more ring furrows than any other *Plaesiacomia* species but, unlike the situation in *Colpocoryphe*, these are shallow and faint.

P. hughesi differs from other *Plaesiacomia* species in lacking paraglabellar areas and having the glabellar furrows very faint or absent, as well as by the relatively large number of pygidial axial rings.

Plaesiacomia vacuvertis sp. nov.

Plate 23, figs. 6, 8–11; Plate 24, figs. 1–6

Name. From Latin *vacuus*, empty and *vertis*, top of the head; alluding to the absence of lateral glabellar furrows in the later growth stages.

Holotype. SM A87322, internal mould of complete specimen, from Ordovician, Llanvirn, type locality of the Hanadir Shale Member of the Tabuk Formation, Jebel Hanadir, Saudi Arabia (25° 28' 00" N. Lat., 43° 27' 30" E. Long.).

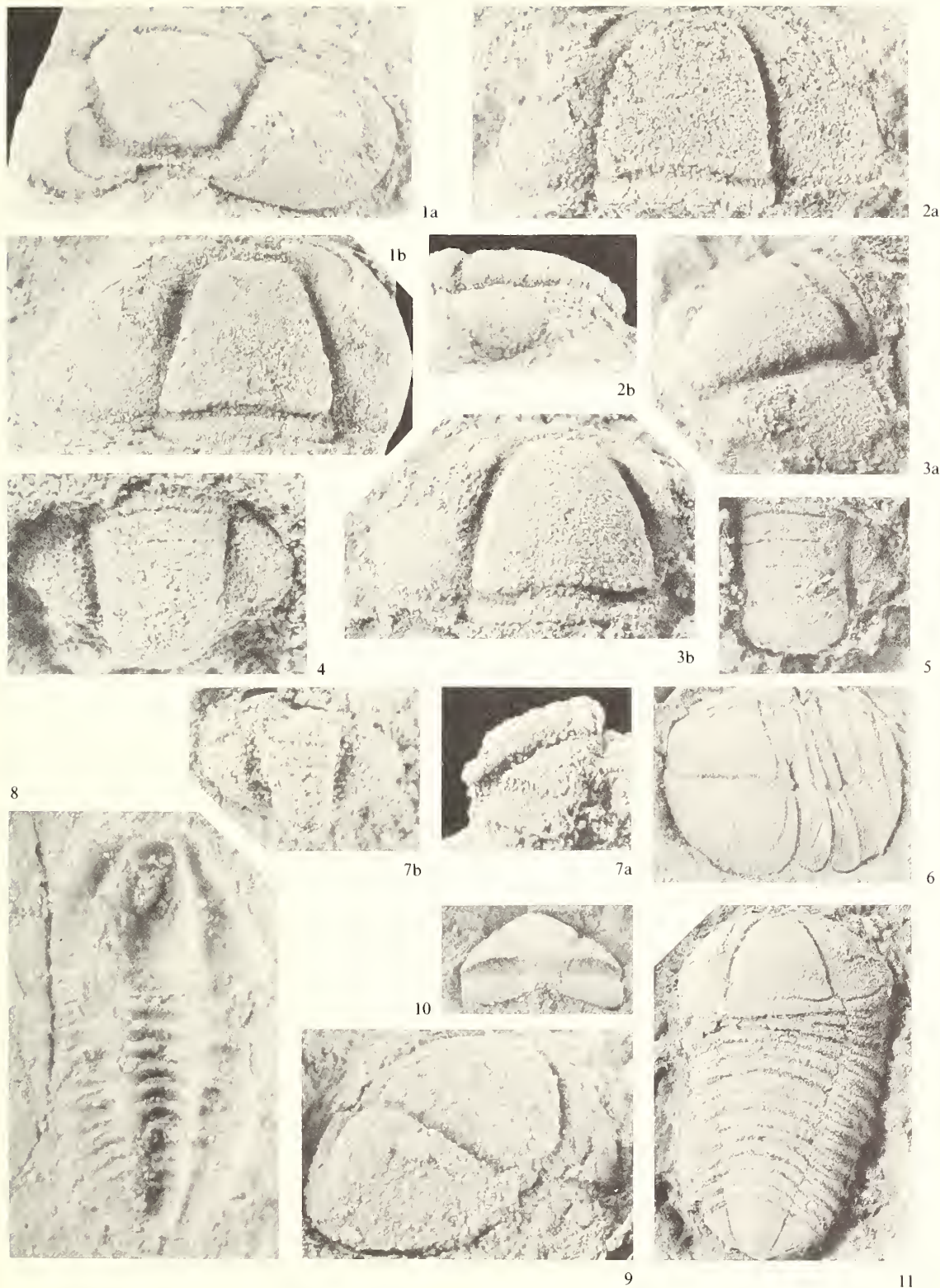
Paratypes. SM A87353, external mould of complete specimen; A87243ab, A87349, A87355, cephalon; A87244, A87321, A87350, partial thoraces and cephalon; A87163ab–A87178ab, A87237ab, A87365, A87294, A87306, A87352, cranidia; A87351, internal mould of incomplete thorax; A87162ab, thoracic segment; A87354, internal mould of pygidium and part of thorax; A87179ab, A87295, pygidia. All from locality and horizon of holotype.

Diagnosis. *Plaesiacomia* species with palpebral lobe placed about half-way along the cephalon. Paraglabellar areas well developed; lateral glabellar furrows weak in smaller individuals, absent in larger ones. Pygidial axis with up to three ring furrows.

EXPLANATION OF PLATE 23

Figs. 1–5, 7. *Plaesiacomia hughesi* sp. nov. Lower Llanvirn, exposure on the left bank in the ravine in the upper reaches of Camnant Brook immediately north of the S bend 230 yd (207 m) S. 13° W. of the fence crossing the stream source, Builth district, Powys (SO 088 575). 1a–b, BM It13815a, internal mould of cephalon, oblique anterior and dorsal views, $\times 6$. 2a–b, BM It13821a, internal mould of cranidium, dorsal and right lateral views, $\times 8$. 3a–b, BM It3024, holotype, internal mould of cranidium, oblique anterolateral and dorsal views, $\times 8$. 4, BM It13820, latex cast from external mould of pygidium, dorsal view, $\times 6$. 5, BM It3026b, latex cast from external mould of pygidium, dorsal view, $\times 8$. 7a–b, BM It13824a, internal mould of pygidium, right lateral and dorsal views, $\times 8$.

Figs. 6, 8–11. *Plaesiacomia vacuvertis* sp. nov. Llanvirn, type locality of the Hanadir Shale Member of the Tabuk Formation, Jebel Hanadir, Saudi Arabia (25° 28' 00" N. Lat., 43° 27' 30" E. Long.). 6, SM A87350, internal mould of incomplete cephalon and thorax, oblique lateral view, $\times 6$. 8, SM A87353, external mould of degree 9? meraspid, ventral view, $\times 20$. 9, SM A87243, internal mould of cephalon, oblique anterolateral view, $\times 8$. 10, SM A87295, internal mould of pygidium, posterior view, $\times 6$. 11, SM A87322, holotype, internal mould of complete specimen, dorsal view, $\times 4$.



THOMAS, homalonotid trilobites

Description. Dorsal exoskeleton more than one and one-half times as long as wide, the maximum width (tr.) situated slightly less than one-third the cephalic length forwards from the posterior cephalic margin. Cephalon semicircular, steeply declined anteriorly and laterally. Occipital ring wide (tr.), trapezoidal, clearly demarcated anteriorly by the occipital furrow. Median occipital tubercle present in some meraspid specimens (Pl. 24, figs. 1, 2, 5). Axial furrows deep and well defined, shallowing posteriorly. Initially they converge at 45° then, anterior to the occipital ring, converge more gently. Preglabellar furrow similar in form to axial furrow and is almost straight (tr.). Glabella tapering forwards to about one-third the width of the occipital ring in larger specimens (Pl. 23, fig. 11). In small meraspid specimens the glabella is subparallel sided, the glabella widening posteriorly during growth (Pl. 24, figs. 5, 2, 1, 4). Up to three pairs of short, faint lateral glabellar furrows are seen in some meraspid specimens (e.g. Pl. 24, fig. 3) but these become effaced in later growth stages. Paraglabellar areas oval, not deeply impressed, their length (exsag.) about one-quarter that of the glabella. Paraglabellar areas are not clearly seen in meraspid specimens but are marked in larger specimens by a distinct flexure in the axial furrow (Pl. 23, fig. 11; Pl. 24, fig. 4). Anterior arch shallow, frontal area narrow (sag.), broadening (exsag.) slightly abaxially. Immediately adjacent to the axial furrow the posterior border is the same width (exsag.) as the occipital ring but it expands somewhat abaxially. Posterior border deep on adaxial two-thirds of fixed cheek, becoming fainter abaxially and terminating near the lateral margin. Posterior branch of facial suture strongly curved, normal to axial furrow at first, then backwardly flexed. Anterior branch of facial suture straight. Palpebral lobe placed near anterior end of glabella in smallest specimens (e.g. Pl. 24, fig. 5), migrating backwards through ontogeny to assume its adult position. Rostral suture straight (tr.).

Hypostome and rostral plate unknown.

Thorax with well-defined trilobation. Axis comprising two-thirds the anterior width (in large specimens), tapering to about half posteriorly. Axis rather narrower

EXPLANATION OF PLATE 24

Figs. 1-6. *Plaesiacomia vacuvertis* sp. nov. Llanvirn, type locality of the Hanadir Shale Member of the Tabuk Formation, Jebel Hanadir, Saudi Arabia ($25^\circ 28' 00''$ N. Lat., $43^\circ 27' 30''$ E. Long.). 1, SM A87166a, internal mould of cranidium, dorsal view, $\times 20$. 2, SM A87167a and A87168a, internal moulds of cranidia, dorsal views, $\times 20$. 3, SM A87163a, internal mould of cranidium, dorsal view, $\times 20$. 4, SM A87172a, internal mould of cranidium, dorsal view, $\times 20$. 5, SM A87170a, internal mould of cranidium, dorsal view, $\times 20$. 6, SM A87179a, internal mould of pygidium, dorsal view, $\times 30$.

Figs. 7-9, 11. *Platycoryphe dyaulax* sp. nov. 7-9, from *convolutus* Zone, Idwian, Llandovery, Qusayba Shale, Qusayba district, Saudi Arabia ($26^\circ 53' 54''$ N. Lat., $43^\circ 32' 15''$ E. Long.). 11, from Qusayba Shale, Qusayba district (exact locality unknown). 7, SM A87542, external mould of cephalon and internal mould of incomplete thorax, ventral and dorsal views, $\times 2$. 8, SM A81820, holotype, cranidium, dorsal view, $\times 2$. 9, SM A87541, pygidium, slightly oblique posterodorsal view, $\times 3$. 11, SM A89859, internal mould of thorax and pygidium, dorsal view, $\times 3$.

Fig. 10. *Brongniartella* sp. Dufton Shale, lower Longvillian, south side of valley 780 yd (702 m) at 142° from Dufton Pike, British Lake District (NY 7042 2605). GSM PJ4549, cranidium, oblique lateral view, $\times 4$.

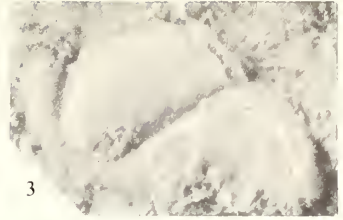
Fig. 12a-b. *Trimerus cylindricus* Salter, 1865. Woolhope Limestone (lower Wenlock), Little Hope, Woolhope district, Hereford and Worcester (Herefordshire). BM I5308, incomplete enrolled thorax, dorsal and right lateral views, $\times 1$.



1



2



3



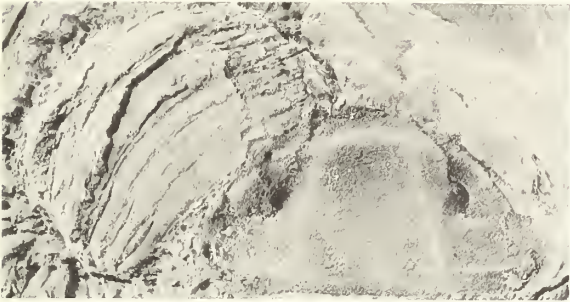
6



5



4



7



8



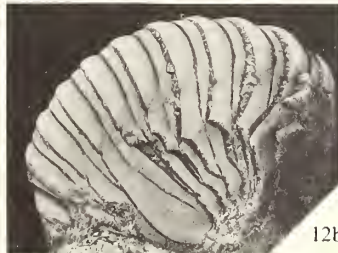
11



10



9



12b



12a

THOMAS, homalonotid trilobites

in meraspids (compare Pl. 23, figs. 8 and 11). Pleural furrow directed slightly posteriorly and becomes progressively fainter abaxially. The pleura is thus divided into two portions of subequal size. Pleural furrow becomes forwardly directed at the fulcrum, portion of furrow on articulating facet shallower and narrower than that on the more proximal part of the pleura (Pl. 23, fig. 6).

Holaspid pygidium about one-third as long (sag.) as the cranidium. Axis constituting almost half the pygidial width, defined by posteriorly converging, deep axial furrows. Ring furrows faint, barely extending to axial furrow in holaspids; much more distinct in meraspids (compare Pl. 23, fig. 11 with Pl. 24, fig. 6). Larger specimens have unfurrowed pleural areas but at least four pairs of pleural ribs are present in meraspids (Pl. 24, fig. 6). Pleural areas small and triangular in holaspids, with deep border furrow. Latter widest and deepest anteriorly, becoming narrower and shallower as it nears the axis (Pl. 23, fig. 10). Border not developed in meraspid individuals.

Discussion. *P. vacuvertis* is most similar to *P. oehlerti* and *P. rara* but the palpebral lobe is placed further forwards than in the former species and further backwards than in the latter. The lateral glabellar furrows are weaker than in either species.

The only previous descriptions of juvenile homalonotids have been of homalonotines (Cooper 1935; Morzadec 1969; Saul 1967; Sheng 1964). It is interesting to note that no border is developed in *P. vacuvertis* meraspides. The deep border furrow in colpocoryphines is associated with enrolment and overlap of the pygidium by the cephalon in holaspids; no such overlap is possible in meraspids.

Subfamily HOMALONOTINAE

[= Portagininae Lespérance, 1968 (*nom. transl.* Bergström, 1973;
ex Portaginidae Lespérance, 1968)]

Diagnosis. Cephalon subtriangular or semicircular, usually without border. Glabella trapezoidal, often ill defined. Glabellar furrows indistinct, may be absent. Paraglabellar areas usually defined. Posterior branch of facial suture intersecting margin at, or anterior of, rounded genal angle; genal spine very rarely developed. Trilobation often indistinct with very wide axis, though axis may be only moderately wide in Ordovician representatives. Pygidium triangular to semicircular, with tendency to reduced distinctness of trilobation.

Remarks. Genal spines in members of this subfamily are known only in two specimens of *Brongniartella* (e.g. Pl. 24, fig. 10). In contrast to the condition in *Bavarilla*, the facial sutures are proparian. Some Devonian homalonotines may also have proparian sutures.

Genera. *Homalonotus* König, 1825, *Brongniartella*, *Burmeisteria*, *Burmeisterella*, *Digonus*, *Dipleura*, *Parahomalonotus*, *Platycoryphe*, *Trimerus*.

Discussion. *Platycoryphe* was placed in the Eohomalonotinae by various authors (e.g. Hughes 1969; Henry 1971; Apollonov 1974) and *Brongniartella* in the same subfamily by Sdzuy (*in* Moore 1959). These genera show few close similarities to *Calymenella* or *Eohomalonotus* but differ from younger genera only in the more

pronounced trilobation and presence of distinct lateral glabellar furrows in some species. Consequently I regard them as homalonotines.

Genus PLATYCORYPHE Foerste, 1919

Type species. *Calymene platycephala* Foerste, 1910, pp. 81–82, pl. 2, fig. 7; pl. 3, fig. 21; from the Trenton (middle Ordovician) of Clifton, Tennessee; by monotypy.

Other species. *P. barroisi* (Lebesconte, 1887); *P. bohemicus* (Barrande, 1852); *P. christyi* (Hall, 1860); *P. dangeardi* Henry, 1971; *P. dentatus* Dean, 1961; *P. dubius* Savage, 1913; *P. dyaulax* sp. nov.; *P. herberti* (Lebesconte, 1887); *P. sinensis* (Lu, 1963); *P. vulcani* (Murchison, 1839); ?*P. convergens* Dean, 1966a.

Diagnosis. Glabella elongate, trapezoidal in outline, with two to three pairs of glabellar furrows. Frontal area relatively short (sag. and exsag.). Cephalic axial furrows straight or with slightly convex-outwards curvature. Thoracic axis wide or moderately wide. Pygidium wider than long; rounded posteriorly; with eight or fewer ring furrows and six or fewer pleural furrows which become fainter posteriorly.

Platycoryphe dyaulax sp. nov.

Plate 24, figs. 7–9, 11

Name. From Greek *dyo*, two and *aulax*, furrow; alluding to the number of lateral glabellar furrows.

Holotype. SM A81820, cephalon, from *convolutus* Zone, Idwian Stage, Llandovery Series, Qusayba Shale Member of the Tabuk Formation, Qusayba district, Saudi Arabia (26° 53' 54" N. Lat., 43° 32' 15" E. Long.).

Paratypes. From the type locality: SM A87542, internal mould of incomplete thorax and external mould of cephalon; A87541, A87543ab, A87754ab, pygidia. From Qusayba district, 22 m below top of Qusayba Shale (26° 53' 30" N. Lat., 43° 32' 30" E. Long.): A87117ab, cephalon. From Qusayba district, 8 m below top of Qusayba Shale (26° 50' 30" N. Lat., 43° 35' 15" E. Long.): A87772, incomplete cephalon; A87920, cranidium. From Qusayba Shale, Qusayba district (exact locality unknown): A87859, internal mould of thorax and pygidium.

Diagnosis. *Platycoryphe* species with two pairs of broad, shallow glabellar furrows. Thoracic axis broad (tr.). Pygidium with six axial rings and five pairs of pleural ribs.

Description. Cephalon subtriangular, slightly less than twice as wide as long, rounded anteriorly. Breadth (tr.) of occipital ring slightly less than half the maximum cephalic width and slightly greater than the glabellar length. Occipital ring trapezoidal, narrowing forwards, bounded anteriorly by well-defined occipital furrow. Occipital furrow narrow abaxially but broader and shallow along the sagittal line. Axial furrows broad and shallow, strongly convergent at first (at approximately 45° to the posterior margin), then converging more gently. Glabella narrows anteriorly to slightly more than half its posterior width, median raised area present along the sagittal line. 1p broad and shallow, posteriorly directed, not confluent with axial furrow. 2p arises opposite the anterior end of the palpebral lobe, is broad and shallow and orientated parallel to 1p. Adaxially posterior border is the same width (exsag.) as the occipital ring, broadening slightly abaxially. Posterior border furrow broad, shallow, terminating near the rounded genal angle. Paraglabellar area very faint, oval, about one-quarter the glabellar length. Frontal area flat and wide (tr.). Anterior branches of facial suture diverge backwards at first then, behind the frontal area, lie subparallel to an exsagittal line. Posterior branch of facial suture strongly curved at

first, running normal to the sagittal line; then sharply recurved. Free cheek triangular in plan view, steeply sloping to lateral border. Lateral border narrows posteriorly, defined by broad, shallow lateral border furrow.

Hypostome unknown. Rostral plate only known from narrow (sag. and exsag.) dorsal portion (Pl. 24, fig. 8).

Thorax with indistinct trilobation. Axis broad, about half the thoracic width. Pleural furrow deep and narrow; posteriorly directed adaxially, becoming parallel to the segment margins abaxially, then directed forwards on the expanded pleural tip.

Pygidium slightly wider than long, rounded posteriorly. Axis infundibular, poorly defined. Ring furrows become shallower on margins of the axis. Pleural furrows directed only slightly backwards, terminating close to the pygidial margin.

Discussion. Most *Platycoryphe* species have three pairs of distinct lateral glabellar furrows—but these are variably developed in some species (see Whittington 1965, p. 488; Henry 1971, p. 70), especially *P. vulcani* (see Whittard 1961, pl. 22, figs. 12, 16; Hughes 1969, p. 97, pl. 14, figs. 3, 6). *P. dyaulax* is most similar to the latter species but differs in having a much wider thoracic axis and less deeply impressed axial furrows. The pygidium of *dyaulax* is more rounded in outline and the axial, ring, and pleural furrows are much shallower than those of *vulcani* (see Whittard 1961, pl. 22, figs. 8–19).

P. dyaulax is closely comparable with *Brongniartella* and *Trimerus* species, as well as with other species of *Platycoryphe*. From species of *Brongniartella* the cephalon differs principally in lacking indented axial furrows. The *Brongniartella* pygidium is distinguished by being longer than wide with a well-defined axis and nine to twelve axial rings. With other species of *Platycoryphe*, *P. dyaulax* shares the straight cephalic axial furrows, posteriorly rounded pygidium (similar to that of *Brongniartella* but with fewer segments) and a similar occipital ring. The cephalon of *P. dyaulax* is similar to that of some *Trimerus* species, the principal differences being in the pygidium—that of *Trimerus* being characteristically longer than wide and pointed posteriorly. With *Trimerus*, and Silurian–Devonian homalonotids in general, *P. dyaulax* shares the wide thoracic axis.

The mosaic of characters seen in *P. dyaulax* is taken to imply a phyletic relationship between *Brongniartella*/*Platycoryphe* and later homalonotines. Because of this mosaic of characters, reference of *dyaulax* to an existing genus is to some extent both arbitrary and subjective. It has been placed in *Platycoryphe* rather than either *Brongniartella* or *Trimerus* because in this way the minimum disruption is caused to the present concept of these genera.

It is likely that the previously apparently well-defined morphological discontinuity between Ordovician and Silurian–Devonian homalonotids was due to the rarity of Llandovery representatives. Apart from *P. dyaulax* I am aware of only seven records of possible Llandovery homalonotids. *Brongniartella* is known from the lower Llandovery of South Wales (Temple 1975) and from beds of questionable Llandovery age in southern Jordan (Wolfart *et al.* 1968). Wolfart (1961) described a Llandovery *Trimerus* species from Paraguay. The specimens (SM A65437–65438) of '*Homalonotus*' recorded by Jones (1925, p. 370) from the Fronian and Telychian of the Llandovery area are poorly preserved but probably represent a *Trimerus* species.

Yin (1966, p. 297) listed '*Homalonotus* sp.' from the *persculptus* Zone of the Upper Yangtze Province—the genus *Liangshanaspis* was later proposed for this material (see discussion p. 160). The specimen (SM A38734ab) from the British Lake District, listed as '*Homalonotus*?' by Marr and Nicholson (1888, p. 664), is not homalonotid. The record of '*Homalonotus* sp.' by Pocock *et al.* (1938, p. 269) rests on a fragment of a thoracic segment (GSM D34473) which is not homalonotid.

PHYLOGENY OF THE HOMALONOTIDAE

The Cambrian ancestors of homalonotids are unknown but a number of Cambrian genera occur in which the over-all morphology, especially the forwardly narrowing glabella and opisthoparian sutures, is similar to that of early calymenids and homalonotids. Warburg (1925, p. 69) noted the similarity of the Calymenacea to *Ptychoparia* and its allies, while Shirley (1931, pp. 8–9) pointed to the similarities shared with ptychopariids in general and *Alokistocare* and *Acrocephalites* in particular. The resemblance of *Lobocephalina* (Conocephaloninae; see Moore 1959, pp. 0237–0238, fig. 176.2c) and *Modocia* (Marjumiidae; see Moore 1959, p. 0306, fig. 228.2a–d) to early homalonotids, especially *Bavarilla*, is also striking. Apart from the glabellar shape and sutural morphology these forms display the tendency to reduced distinctness of glabellar furrows, relatively short genal spines, small eyes (in *Modocia*), thorax of fourteen segments with rounded pleural tips, and a posteriorly rounded pygidium which possesses an ill-defined border.

By the Tremadoc/Arenig a number of genera occur from which evolutionary lines lead to younger calymenids and homalonotids. The difficulty of classifying these early genera has been discussed and is indicative of their common origin.

In the Arenig representatives of the Colpocoryphinae, Eohomalonotinae, and Homalonotinae are present, the colpocoryphines and eohomalonotines becoming extinct in the Caradoc and Ashgill respectively. Homalonotines persist until the middle Devonian though they are rare in the Ashgill and even more so in the Llandovery (see pp. 170–171). *Trimerus* first appears in the upper Llandovery and seems to have given rise to younger genera. A new radiation began in the upper Silurian (three genera) and continued in the lower Devonian (six genera). The stratigraphical ranges of the Devonian genera are imprecisely known but on present evidence *Trimerus* disappears in the Siegenian while *Parahomalonotus*, *Burmeisterella*, *Burmeisteria*, and *Digonus* are restricted to the interval Gedinnian to Emsian. Only *Dipleura* is certainly known from the middle Devonian. These genera are in need of revision but show many similarities to *Trimerus* and *Dipleura* and were probably derived from one or both of these genera. The cephalon of *Burmeisteria*, for instance, shares many features with juvenile specimens of *Dipleura* (compare Morzadec 1969, pl. 2, fig. 6a with Moore 1959, p. 0460, fig. 361.1a). The form of the glabella and lateral glabellar furrows are exceedingly similar and *Burmeisteria* may be a neotenus descendant of *Dipleura*.

As far as Ordovician forms are concerned, *Colpocoryphe* and *Plaesiacomia* share many common characters, some of which are due to the presence of coaptative structures associated with enrolment. Many of the features of *Colpocoryphe* are present in a more extreme form in *Plaesiacomia*—the tendency to efface glabellar

furrows and loss of distinct pygidial segmentation, for instance—and I regard *Plaesiacomia* as being derived from early *Colpocoryphe* species. *Colpocoryphe* displays some 'primitive' features concordant with this view in that strong eye ridges are often developed and paraglabellar areas absent (Dean 1966b, p. 141). The evidence is inconclusive, however, since the oldest *Plaesiacomia* species have smooth cephalae without eye ridges and resemble *Colpocoryphe* mainly in having a relatively large number of pygidial axial rings.

Fortey (1974, pp. 61–65, pl. 20, figs. 1–12) described the unusual olenid *Svalbardites hamus*, from the Arenig of Spitsbergen, and noted (p. 64) the similarity of its pygidium to those of *Plaesiacomia* species, although he doubted a direct relationship. The form of the colpocoryphine pygidium is largely determined by its role in enrolment, and the lack of a deep border furrow in *Svalbardites* suggests that the resemblance is superficial. There is also some cephalic similarity, notably in eye position and general effacement, but the *Svalbardites* glabella is completely unlike the forwardly tapering form characteristic of homalonotids. Homalonotids have a well-developed rostral plate, olenids commonly have no rostral plate and the free cheeks are united by a narrow strip of doublure. I consider an olenid-homalonotid relationship unlikely and the similarities between *Plaesiacomia* and *Svalbardites* to be superficial.

Eohomalonotus and *Calymenella* form a distinct group. Some early species of *Platycoryphe* resemble *Calymenella* in having distinct eye ridges and a sigmoidal 1p furrow (see Henry 1971). In other respects (no distinct cephalic border; pygidial form; no prominent pygidial interpleural furrows), however, they are closer to later species of *Platycoryphe*. Such forms seem to be close to the point of divergence of homalonotines and eohomalonotines.

Platycoryphe and *Brongniartella* are similar genera and the difficulty of discriminating between them when the glabellar furrows are weak has often been noted (Dean 1961, p. 344; Whittington 1965, p. 488; Hughes 1969, p. 98). The resemblances are unsurprising since *Brongniartella* may have been derived from *Platycoryphe* (Whittington 1966b, p. 723, text-fig. 13). The Llandovery homalonotine, *P. dyaulax*, shows features in common with both younger homalonotids and with *Platycoryphe* and *Brongniartella*. I consider that post-Ordovician homalonotines were derived from this stock. Sdzuy (1957, p. 284) suggested that the pygidial morphology of *Brongniartella* indicated that it did not give rise to younger genera. He did not develop this theme, and *Platycoryphe* was not discussed. Sdzuy (p. 286, fig. 3) derived *Trimerus* from *Eohomalonotus* but, because of the morphological differences discussed above, this view is considered untenable.

Silurian–Devonian homalonotines comprise a closely related, morphologically homogeneous group (for a summary of their relationships see Tomczykowa 1975). The Ludlow genus *Homalonotus* may have evolved from an upper Wenlock form like *T. johannis* by the loss of glabellar lobation together with a reduction in length, and folding, of the frontal area. Other features of the exoskeleton are very similar (compare Salter 1865, pl. 12, figs. 2–10 and pl. 13, fig. 8 with pl. 12, fig. 11 and pl. 13, figs. 1–7). Tomczykowa (1975, p. 14) suggested that *T. johannis* might also be ancestral to *Digonus*. Such a relationship is plausible but a substantial stratigraphical gap exists between the occurrence of *T. johannis* and the earliest record of *Digonus* in the

Gedinnian. *Dipleura* first appears in the Ludlow and may have been derived from *Trimerus* through a form similar to *T. lobatus* Tomczykowa, 1975.

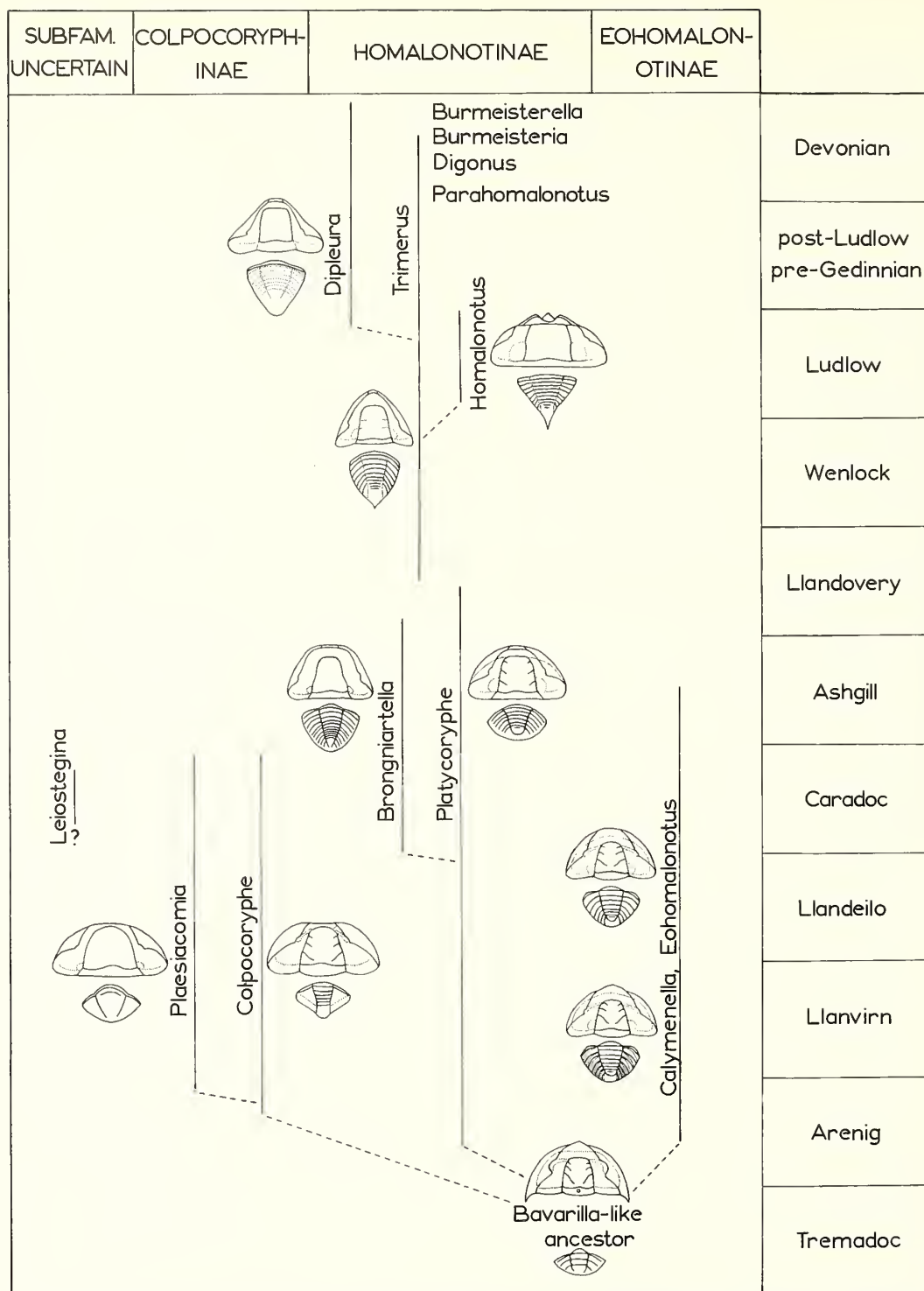
Throughout the Ordovician, and in the early Silurian, homalonotines display a progressive increase in the width (tr.) of the thoracic axis and a tendency to reduced distinctness of trilobation. By the middle Silurian the thoracic axis is very wide and trilobation quite indistinct. The thoracic segments of homalonotines and colpocoryphines differ from those of all other trilobites in that the articulating and pleural furrows merge and the articulating half ring becomes fused with the anterior pleural band. Hence the articulating half ring becomes greatly enlarged (tr.) and comes to occupy much of the width of the segment (see Pl. 24, fig. 12a-b). Material of *Calymenella* loaned to me by Professor H. B. Whittington indicates that eohomalonotines differ from other homalonotids in this respect. They have a more 'normal' type of articulation, the articulating half rings not extending outside the axis (see also Sdzuy 1957, pl. 1, fig. 8). This phenomenon is associated with the retention of a relatively narrow thoracic axis in eohomalonotines.

The selective forces responsible for the evolutionary changes outlined above are unknown. The adoption of a rather specialized mode of life may explain the morphological contrasts between the Colpocoryphinae/Homalonotinae and their inferred ancestor, *Bavarilla*.

The similarity of Silurian-Devonian genera suggests that the post-Ordovician homalonotine radiation was connected with the exploitation of a number of closely related niches, the general mode of life being broadly similar. *Homalonotus* is the most unusual post-Ordovician homalonotine. The complex structure of the anterior part of the cephalon (see Salter 1865, pl. 12, fig. 2) may indicate that this genus had somewhat different life habits.

Eohomalonotines change little throughout their history and show few major differences from *Bavarilla*. They appear to represent a group whose way of life changed little from that of their ancestors. The retention of several 'primitive' characters (e.g. eye ridges, anteriorly widened border, sigmoidal lp furrow, relatively small rostral plate, thoracic morphology) accords with this view. A case could therefore be argued for placing the colpocoryphines and homalonotines in a separate family from the Eohomalonotinae and *Bavarilla*. This reflects the inferred phylogeny in which the eohomalonotines represent a relatively unchanged conservative stock while the Colpocoryphinae and Homalonotinae are 'progressive' groups united, in particular, by their thoracic structure. While such an arrangement is in some ways appealing, its adoption would be premature. The pattern outlined may need modification when relationships between homalonotids and calymenids in general, and between *Bavarilla* and older genera, are better understood.

What is known of homalonotid distribution supports the proposed phylogeny. Whittington (1966b, 1972) and Whittington and Hughes (1972, 1973) have demonstrated the existence of discrete faunal provinces in which different trilobite groups evolved in relative isolation through much of Ordovician time. In the Arenig-Llandeilo *Colpocoryphe*, *Plaesiacomia*, *Eohomalonotus*, *Calymenella*, and *Platycoryphe* are restricted to the Florida/west-central Europe/North Africa region (the Selenopeltis province), a part of which *Bavarilla* inhabited in the Tremadoc. The upper Ordovician decay of faunal provincialism is reflected in homalonotid



TEXT-FIG. 1. Phylogeny of the Homalonotidae. Solid lines represent known ranges of genera, broken ones their inferred relationship.

distribution with *Brongniartella* and *Platycoryphe* extending their range into North America and Kazakhstan during the Caradoc and Ashgill. In the Ashgill *Brongniartella* is widespread in northern Europe, *Calymenella* being present in central China (Whittington 1966b, p. 728) and possibly Argentina (Baldis and Blasco 1975).

Some of the unusual features of *Leiestegina*, from the Caradoc of Bolivia, may be due to its having evolved in relative isolation. According to Whittington and Hughes's (1972, p. 257, fig. 9) palaeogeographical map Bolivia lay on the opposite side of Gondwanaland to the Selenopeltis fauna, although at a similar latitude.

No marked provincialism is developed in the Silurian. *Platycoryphe* occurs in the Llandovery of Saudi Arabia and China and *Brongniartella* in the low Llandovery of South Wales. *Trimerus* first occurs in the upper Llandovery of South Wales and Paraguay and extends its range in the later Silurian and lower Devonian, being known from North America, Europe, Mongolia, and Australia. *Homalonotus* first appears in the lower Ludlow of South Wales and throughout its short range was restricted to Nova Scotia, Britain, Scandinavia, and Poland. On a pre-drift map these areas lie close together some 10°–20° south of the equator. *Dipleura* is first known from the upper Ludlow of Britain and Poland and was probably derived from one of the *Trimerus* species found in this area. Homalonotids are widespread in the Devonian but it is not possible to discuss the distribution of individual genera since the taxonomy is poorly known.

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Note on orientation. Dorsal view refers to the orientation in which cephalons are placed with the occipital ring in a vertical plane and pygidia placed with the anterior margin of the axis vertical.

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DINOFLAGELLATE CYSTS FROM THE BEARPAW FORMATION (?UPPER CAMPANIAN TO MAASTRICHTIAN) OF MONTANA

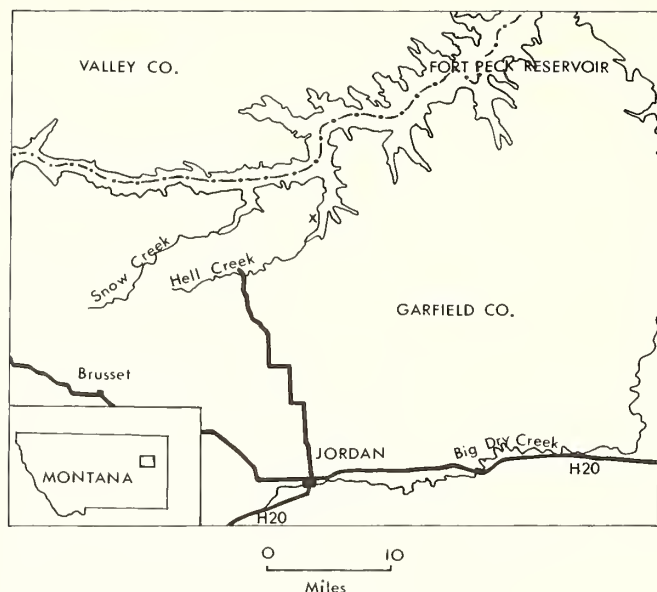
by REX HARLAND

ABSTRACT. A dinoflagellate cyst assemblage is described from the Bearpaw Formation of Montana, U.S.A. *Deflandrea montanaensis* sp. nov. is described. Archeopyle formation in *Senegalinium tricuspis* (O. Wetzel) comb. nov. is demonstrated to be of the large intercalary type, and this, together with its basic cavate morphology, allows for the recombination of the species. Also recombined are *S. magnifica* (Stanley), ?*S. albertii* (Corradini), *S. boloniensis* (Riegel), *S. gaditanum* (Riegel), ?*S. kozlowskii* (Gorka), *S. pannuceum* (Stanley), *S. pentagonalis* (Corradini), and *S. subquadratum* (Corradini). The Bearpaw Formation in Montana, on radiometric and on dinoflagellate cyst evidence is younger than that seen in southern Alberta, and may include strata encompassing the Campanian-Maastrichtian boundary.

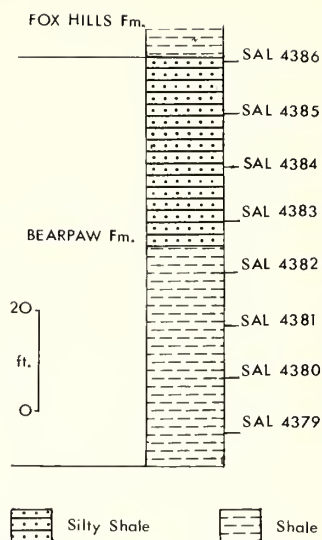
THE Bearpaw Formation of the northern U.S.A. and Canada was deposited during the last major transgression of the Late Cretaceous sea, and before sedimentation was influenced by the growth of alluvial plains from the newly uplifted Cordillera (Stelck 1967). The base of the formation is known to be of Late Campanian age in both southern Alberta and Saskatchewan, Canada (Caldwell 1968). In Saskatchewan the formation is believed to extend into the Maastrichtian, whereas in southern Alberta it is restricted to the Campanian. A potassium-argon date of 75 ± 4 million years is available on a bentonite close to the base of the formation at Lethbridge, Alberta (Folinsbee *et al.* 1960, 1961), and is indicative of a Late Cretaceous age (Casey 1964; Lambert 1971).

Norton and Hall (1969) state that the Bearpaw Formation at Hell Creek, Montana, U.S.A., is Late Cretaceous in age and report a date of 70 million years from a position close to the level of their sample KB-1, i.e. close to the base of the unit as seen at Hell Creek. This suggests that the section in Montana is somewhat younger than that in southern Alberta and is probably equivalent to the upper part of the section in Saskatchewan close to, if it does not contain, the Campanian-Maastrichtian boundary, i.e. 70 m.y. or 72 m.y. (Casey 1964 and Lambert 1971 respectively). Recently Obradovich and Cobban (1975) in discussing a time-scale for the Late Cretaceous of North America suggest a 70-71 m.y. date for the Campanian-Maastrichtian boundary, but admit difficulty in defining the boundary palaeontologically. Harland (1973) following Caldwell (1968) accepted the base of the *Baculites baculus* Zone as the Campanian-Maastrichtian boundary but Obradovich and Cobban (1975) suggest it may fall as low as the base of the *B. reesidei* Zone, i.e. much of the southern Alberta Bearpaw would then be Maastrichtian. This view is not accepted here.

The present study was undertaken to describe and compare the dinoflagellate cyst assemblage from Montana with that published from southern Alberta (Harland 1973). The southern Alberta outcrop is some 230 miles north-west of the Montana section.



TEXT-FIG. 1. Sketch map of a part of the Fort Peck Reservoir in north-eastern Montana, U.S.A. to show the position of the sample locality (marked with an X). Bold lines indicate roads.



TEXT-FIG. 2. A stratigraphical section of the Bearpaw Formation at the Hell Creek locality showing the position of the samples.

MATERIALS AND METHODS

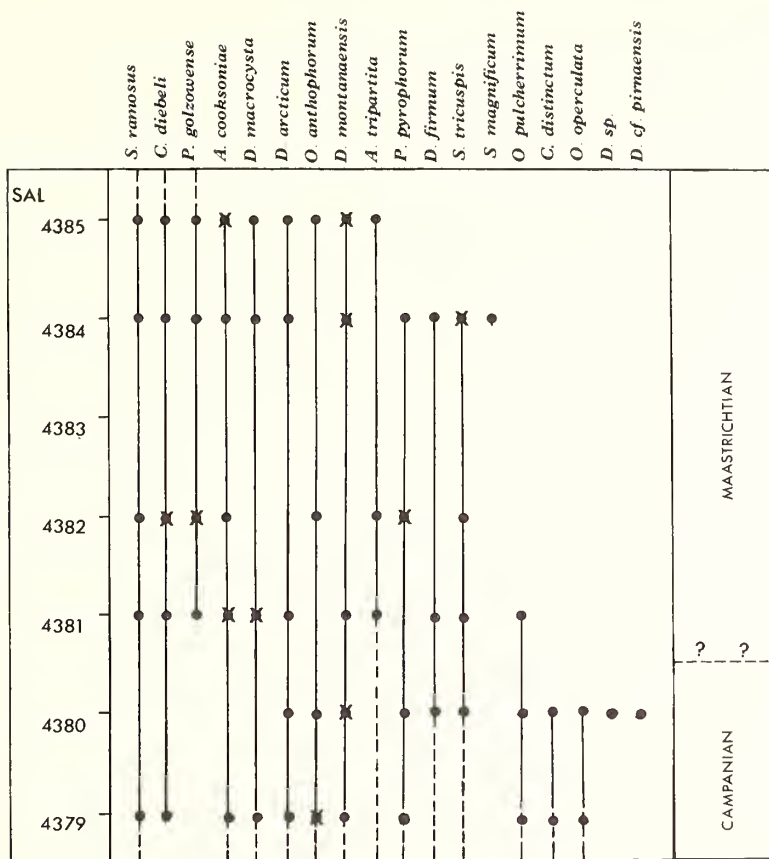
In June 1969 Drs. G. Playford, University of Queensland, Australia, and G. D. Williams, University of Alberta, Canada, collected eight samples of Bearpaw Formation from the banks of the Fort Peck Reservoir, Montana, U.S.A., i.e. locality 1 of Norton and Hall (1969). This locality (text-fig. 1) is situated some 22 miles north of Jordan on the Hell Creek part of the reservoir at S $\frac{1}{2}$, Sect. 31, T22N, R37E, Garfield County, Montana. At the time of collection 70 ft (21.33 m) of Bearpaw was exposed above the water level in the reservoir and beneath the overlying Fox Hills Formation. Norton and Hall (1969) described the distinct lithological change from the dark Bearpaw shale to the light-coloured shales and sandstones of the Fox Hills sandstone but no unconformity was noted. The Bearpaw Formation at this locality can be divided into a lower shale unit and an upper silty shale unit and both appear as very dark rock when freshly exposed (Norton and Hall 1969).

The sample distribution through the section is shown in text-fig. 2; the samples have been registered in the Palynological Collections of the Institute of Geological Sciences (I.G.S.) at Leeds as SAL 4379-SAL 4386. All eight samples were processed using standard palynological techniques, but beyond the hydrofluoric acid stage the residues were handled using the filtration system of Neves and Dale (1963).

Where dimensions are quoted the figure in parenthesis is the arithmetic mean of the measured morphological parameters. All illustrated material is registered in the MPK series of the palynological collections of the I.G.S. at Leeds. The ranges of species as quoted from Harker and Sarjeant (1975) are compilations from their tables in order to indicate the world-wide range.

SYSTEMATICS

The dinoflagellate cysts of this paper are placed within either a gonyaulacacean or peridiniacean grouping. It is felt that although the emended supra-generic classification of Sarjeant and Downie (1974) goes a long way to answering the criticisms of



TEXT-FIG. 3. The range of species through the Bearpaw Formation at the Hell Creek locality, Fort Peck Reservoir, Montana, showing the possible Campanian-Maastrichtian boundary. Range of species that are known to be greater than that as proved at Hell Creek are shown by a broken line. The large dots represent the presence of a species within the sample indicated, and the crosses indicate an occurrence of greater than 10% of the dinoflagellate cyst population.

Wall and Dale (1968) there are too many new forms being described and too much taxonomic revision to use it or any other formal supra-generic classification at the present time. This is particularly true of deflandreoid cysts where detailed knowledge of their morphology, particularly archeopyle formation, is still lacking. There is, however, no question that at least two major groupings can be recognized amongst fossil dinoflagellate cysts and these are used here; the Gonyaulacaceae and the Peridiniaceae.

Division PYRRHOPHYTA Pascher
Class DINOPHYCEAE Pascher
Order PERIDINIALES Lindemann

GONYAULACACEAN GROUP

Genus CYCLONEPHELIUM Deflandre and Cookson emend. Williams and Downie 1966

Type species. *Cyclonephelium compactum* Deflandre and Cookson, 1955; O.D.

Cyclonephelium distinctum Deflandre and Cookson, 1955

Plate 25, fig. 14

1955 *Cyclonephelium distinctum* Deflandre and Cookson, pp. 285–286, pl. 2, fig. 14; text-figs. 47, 48.

Figured material. Slide SAL 4381-RH1, specimen MPK 917.

Remarks. Only a few specimens were found in the lower part of the sequence and the illustrated form falls at the smaller end of the size range of this species as quoted by Harland (1973). Sarjeant (1967*a*) gives a Hauterivian to Santonian range for this species but it is now known from the Campanian (Clarke and Verdier 1967; Harland 1973) and from the ?Maastrichtian (McIntyre 1974). Harker and Sarjeant (1975) record a range of Berriasian to ?early Palaeocene.

Genus DICTYOPYXIDIA Eisenack, 1961

Type species. *Dictyopyxidia areolata* (Cookson and Eisenack) Eisenack and Kjellström, 1971; O.D.

Dictyopyxidia sp.

Plate 25, fig. 15

Figured material. Slide SAL 4380-RH1, specimen MPK 918.

Remarks. This appears to be a new species but because only a single specimen was observed its formal description is not attempted. It is closely comparable to *D. circulata* Clarke and Verdier, 1967 but does not appear to have the complexity of fields or the rounded ambitus of that species. It was found towards the base of the section.

Genus OLIGOSPHAERIDIUM Davey and Williams, 1966

Type species. *Oligosphaeridium complex* (White) Davey and Williams, 1966; O.D.

?*Oligosphaeridium anthophorum* (Cookson and Eisenack) Davey, 1969

1958 *Hystichosphaeridium anthophorum* Cookson and Eisenack, pp. 43–44, pl. 11, figs. 12, 13; text-figs. 16–18.

1969 *Oligosphaeridium anthophorum* (Cookson and Eisenack) Davey, pp. 147–148, pl. 5, figs. 1–3.

Remarks. This species was observed throughout the section. Its range, noted as ?Oxfordian to Albian by Sarjeant (1967*a*), is now known to be at least into the ?Maastrichtian (McIntyre 1974), and Harker and Sarjeant (1975) indicate a Berriasian to ?early Oligocene range. It is quite possible, however, that the present assignment is incorrect, as the Jurassic forms, probably like the holotype, have

solid processes (R. J. Davey pers. comm. 1975) whereas these and other Upper Cretaceous forms have hollow processes. This species could, therefore, benefit from restudy and it is quite likely that these and other Late Cretaceous forms are a separate, possibly new, species.

Oligosphaeridium pulcherrimum (Deflandre and Cookson) Davey and Williams, 1966

1955 *Hystriosphæridium pulcherrimum* Deflandre and Cookson, pp. 270–271, pl. 1, fig. 8; text-figs. 21, 22.

1966 *Oligosphaeridium pulcherrimum* (Deflandre and Cookson) Davey and Williams, pp. 75–76, pl. 10, fig. 9; pl. 11, fig. 5.

Remarks. This form was recorded from the lower part of the sequence but its range (Sarjeant 1967a) is Valanginian to lower Eocene. It was recorded from the Bearpaw of southern Alberta (Harland 1973) and more recently from the Campanian and Maastrichtian of Arctic Canada (McIntyre 1974). Harker and Sarjeant (1975) indicate a ?Jurassic to ?middle Eocene range; middle Albian to late Campanian in North America.

Genus SPINIFERITES Mantell emend. Sarjeant 1970

Type species. *Spiniferites ramosus* (Ehrenberg) Mantell, 1854; S.D. by Loeblich and Loeblich 1966.

Spiniferites ramosus (Ehrenberg) Mantell, 1854

1838 *Xanthidium ramosum* Ehrenberg, pl. 1, figs. 1, 2, 5.

1854 *Spiniferites ramosus* (Ehrenberg) Mantell, p. 239, Lign 77, fig. 4.

Remarks. Specimens of this species complex were recorded in all the samples studied. *S. ramosus* has a Berriasian to Recent stratigraphic range (Harker and Sarjeant 1975).

PERIDINIACEAEN GROUP

Genus AUSTRALIELLA Vozzhennikova, 1967

Type species. *Australiella tripartita* (Cookson and Eisenack) Vozzhennikova, 1967; O.D.

Australiella cooksoniae (Alberti) Vozzhennikova, 1967

Plate 25, fig. 9

1959 *Deflandrea cooksoni* Alberti, 97–98, pl. 9, figs. 1–6.

1967 *Australiella cooksoni* (Alberti) Vozzhennikova; 132, pl. LXI, figs. 1–4.

Figured material. Slide SAL 4385-RH1, specimen MPK 919.

Remarks. Specimens of this species occur throughout the studied sequence. Its recorded range (Sarjeant 1967a) is Santonian to Campanian. McIntyre (1974) recorded a form he referred to as *Deflandrea* sp. cf. *D. cooksoni* from the ?Maastrichtian, and Zaitzeff and Cross (1970) have also recorded it from the Maastrichtian. The form described as *D. korojonensis* Cookson and Eisenack by Harland (1973) should more correctly be assigned here. Harker and Sarjeant (1975) give an ?early Cenomanian to early Palaeocene age for this species.

Australiella tripartita (Cookson and Eisenack) Vozzhennikova, 1967

1960 *Deflandrea tripartita* Cookson and Eisenack, 2, pl. 1, fig. 10.

1967 *Australiella tripartita* (Cookson and Eisenack) Vozzhennikova, pp. 134–135, pl. LXI, fig. 1; pl. LXIV, figs. 1–4.

Remarks. This species was observed throughout the section. Its previously recorded range (Sarjeant 1967a) was Turonian to Campanian, so the present observation may indicate an extension into the lowermost Maastrichtian in North America. Harker and Sarjeant (1975) recently gave an ?early Cenomenian to ?late Maastrichtian range.

Genus CERATIOPSIS Vozzhennikova, 1963

Type species. *Ceratiopsis leptoderma* Vozzhennikova, 1963; O.D.

Ceratiopsis diebeli (Alberti) Vozzhennikova, 1967

Plate 25, fig. 16

1959 *Deflandrea diebeli* Alberti, 99–100, pl. 9, figs. 18–21.

1967 *Ceratiopsis diebeli* (Alberti) Vozzhennikova, pp. 159–160, pl. CXIX, fig. 4.

Figured material. Slide SAL 4384-RH1, specimen MPK 920.

Remarks. This species was found throughout the sequence and had a previously recorded range of Santonian to Campanian (Sarjeant 1967a), it is now known from the Maastrichtian and Danian (Wilson 1971). Harker and Sarjeant (1975) indicate a ?late Coniacian to late Eocene range.

Genus DEFLANDREA Eisenack emend. Williams and Downie 1966

Type species. *Deflandrea phosphoritica* Eisenack, 1938; O.D.

Deflandrea macrocysta Cookson and Eisenack, 1960

1960 *Deflandrea macrocysta* Cookson and Eisenack, 3, pl. 1, figs. 7, 8.

Remarks. *D. macrocysta* is found throughout the section. Sarjeant (1967a) and Harker and Sarjeant (1975) recorded a restricted Campanian range for this species so that the present study may indicate a slight extension into the lowermost Maastrichtian.

Deflandrea montanaensis sp. nov.

Plate 25, figs. 4, 6, 7, 10–12

Diagnosis. Cavate cyst, epitract conical, hypotract hemispheroidal with an asymmetrical 'skirt' and horn. Endoblast elongated apically and hemispheroidal antapically. Wall layers smooth. Apex surmounted by a bifid tip; the larger antapical horn acuminate. Tabulation discernible but not usually recognizable, delimited by low, smooth, or poorly denticulate ridges. Cingulum planar, may or may not be slightly indented; sulcus large and broad, widening towards the antapex. Archeopyle intercalary in periphragm and endophragm; commonly attached Ia/Ia (Evitt 1967), and apically/antapically elongate hexagonal in shape.

Figured material. Holotype: Slide SAL 4380-RH1, specimen MPK 921, Bearpaw Formation, ?Campanian to Maastrichtian, Montana, U.S.A. Paratypes: Slide SAL 4380-RH2, specimens MPK 922–924.

Dimensions. Holotype: length 35.0 μ , breadth 16.25 μ . Range: length 18.75 (27.50) 36.25 μ , breadth 8.75 (17.0) 25.00 μ . Twelve specimens were measured from a studied population of twenty-five.

Description. A diamond-shaped to elongate fusiform cyst made up of the two wall layers that are only adpressed in the cingular region and on the upper part of the hypotract. The epittractal periphragm is drawn out into an apical horn which carries a dorso-ventrally flattened, bifid tip. The antapical 'skirt' and horn sometimes carry small, poorly developed, irregular spines, especially on the margin of the 'skirt'. The tabulation is variously developed but difficult to decipher, it is probably ?4', 1a, ?7'', 6c, ?''', ?2'''''. The cingulum is divided into six well-defined cingular plates. Archeopyle is formed by a single opening through the periphragm and endophragm and the operculum appears to remain attached (Pl. 25, fig. 10), type Ia/Ia of Evitt (1967).

Remarks. This cyst is closely comparable to *Spinidinium clavum* Harland, 1973 (see below for further comments), and it is possible that a full range of variation exists between the two forms. This was not seen to be the case, however, in either the present assemblage or in southern Alberta (Harland 1973), and therefore it is regarded as a distinct and separate species. It occurs throughout the studied section.

Comparisons. This cyst is closely comparable to *D. minor* Alberti, 1959 from which it differs in over-all shape, *D. minor* being more rhomboidal and having a condensed endoblast, and in possessing a tabulation. It is also comparable with *D. bahnei* Cookson and Eisenack, 1962 which again differs in form, in the amount of endoblastic 'contraction' and in possessing spines. It is closest to *S. clavum* Harland, 1973 but differs in not possessing high, denticulate, sutural crests and in being much smaller, i.e. nearly half the size. It may be an evolutionary descendant of that species. It is also closely comparable to *S. rallum* Heisecke, 1970, *D. irmoechinata* Heisecke, 1970, and *D. rhombica* Cookson and Eisenack, 1974, all of which, however, differ in possessing numerous well-developed spines.

Deflandrea cf. *pirnaensis* Alberti, 1959

Plate 25, fig. 8

1959 *Deflandrea pirnaensis* Alberti, p. 100, pl. 8, figs. 1-5.

Figured material. Slide SAL 4381-RH1, specimen MPK 925.

Remarks. The single specimen encountered is most closely comparable to *D. pirnaensis*, which had a previously published range of Albian to Coniacian (Sarjeant 1967a). Harker and Sarjeant (1975) indicate a late Hauterivian to late Maastrichtian range.

Genus *DICONODINIUM* Eisenack and Cookson, 1960

Type species. *Diconodinium multispinum* (Deflandre and Cookson) Eisenack and Cookson, 1960; O.D.

Diconodinium arcticum Manum and Cookson, 1964

1964 *Diconodinium arcticum* Manum and Cookson, pp. 18-19, pl. 6, figs. 1-4.

Remarks. *D. arcticum* occurs throughout the sequence. Its previously recorded range

(Manum and Cookson 1964) was early late Cretaceous which has now been ascertained by Felix and Burbridge (in press) to be a late Cenomanian to early Campanian age. The present evidence and also that of McIntyre (1974) suggests an extension of the range into the ?Maastrichtian. Harker and Sarjeant (1975) indicate an early Cenomanian to late Campanian range.

Diconodinium firmum Harland, 1973

1973 *Diconodinium firmum* Harland, pp. 669–670, pl. 84, figs. 8, 9, 15; text-fig. 6.

Remarks. This form was found almost throughout the sequence. Its previous range was late Campanian (Harland 1973) so that its range may be increased into the ?earliest Maastrichtian (herein and McIntyre 1974). Zaitzeff and Cross (1970) recorded *Diconodinium* sp. 1 which is probably synonymous to *D. firmum* from the Maastrichtian of Texas. After checking the original and comparable specimens of this species (all specimens illustrated in Harland (1973) are now held by the I.G.S. in Leeds) it is thought to have an archeopyle like that illustrated by McIntyre (1975) for his genus *Laciniadinium*, but since some doubt remains a formal recombination is not attempted here.

Genus PALAEOCYSTODINIUM Alberti, 1961

Type species. *Palaeocystodinium golzowense* Alberti, 1961; O.D.

Palaeocystodinium golzowense Alberti, 1961

Plate 25, fig. 13

1961 *Palaeocystodinium golzowense* Alberti, p. 20, pl. 7, figs. 10–12; pl. 12, fig. 16.

Figured material. Slide SAL 4381-RH1, specimen MPK 926.

Remarks. *P. golzowense* is confined to samples above SAL 4380. Its previously recorded range (Sarjeant 1967a) was Eocene to Oligocene but it has also been

EXPLANATION OF PLATE 25

All figures are at a magnification of $\times 500$ unless otherwise stated and were photographed using phase contrast techniques.

Fig. 1. *Palaeoperidinium pyrophorum* (Ehrenberg) Deflandre, MPK 927, dorsal view showing over-all morphology, faint growth lines and slight rupture of the epitract along the cingulum.

Fig. 2. *Senegalium magnificum* (Stanley) comb. nov., MPK 928, specimen showing the large, single reflected plate archeopyle and the small pericoels.

Fig. 3, 5. *Senegalium tricuspis* (O. Wetzel) comb. nov., MPK 929, 930, fig. 3 showing the large intercalary archeopyle.

Figs. 4, 6, 7, 10–12. *Deflandrea montanaensis* sp. nov., MPK 921, 922, 923, 924, figs. 4, 7, holotype, figs. 4, 6, $\times 1000$, specimens showing range of variation and over-all morphology.

Fig. 8. *Deflandrea* cf. *pirnaensis* Alberti, MPK 925.

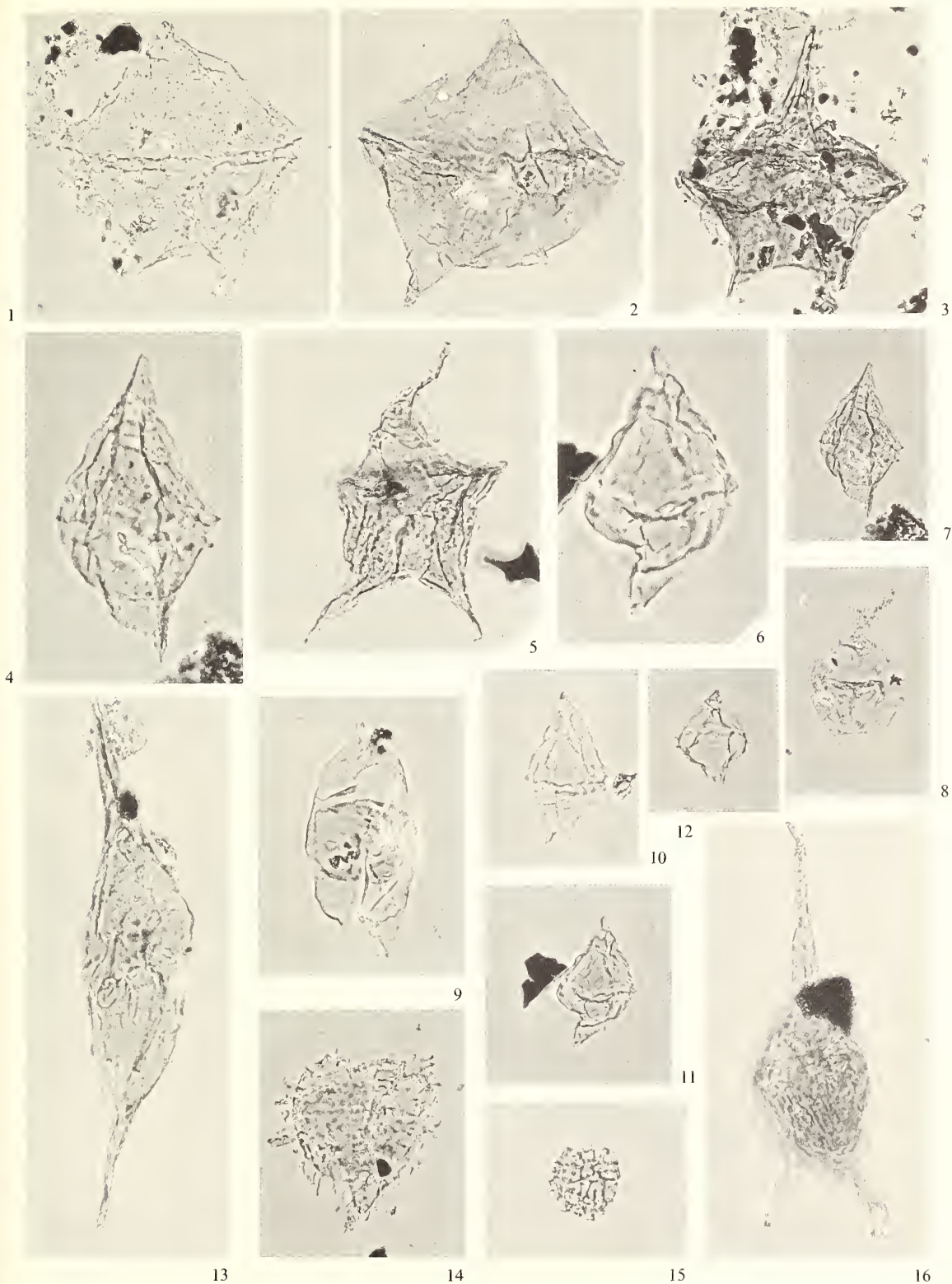
Fig. 9. *Australiella cooksoniae* (Alberti) Vozzhennikova, MPK 919.

Fig. 13. *Palaeocystodinium golzowense* Alberti, MPK 926, specimen showing the intercalary archeopyle.

Fig. 14. *Cyclonephelium distinctum* Deflandre and Cookson, MPK 917.

Fig. 15. *Dictyopyxidina* sp., MPK 918.

Fig. 16. *Ceratiopsis diebeli* (Alberti) Vozzhennikova, MPK 920.



HARLAND, Campanian-Maastrichtian dinoflagellates from Montana

recorded from the Maastrichtian to ?Palaeocene (Malloy 1972). Harker and Sarjeant (1975) record an early Maastrichtian to late Oligocene range.

Genus PALAEOPERIDINIUM Deflandre, 1934

Type species. Palaeoperidinium pyrophorum (Ehrenberg) Deflandre, 1935, emend. Sarjeant 1967b; S.D.

Palaeoperidinium pyrophorum (Ehrenberg) Deflandre, 1935, emend. Sarjeant 1967b

Plate 25, fig. 1

1838 *Peridinium pyrophorum* Ehrenberg, pl. 1, figs. I, IV.

1967b *Palaeoperidinium pyrophorum* (Ehrenberg) Sarjeant, pp. 246–247, figs. 1–6.

Figured material. Slide SAL 4379-RH1, specimen MPK 927.

Remarks. This cyst is found throughout the studied section. Its previously recorded range was Coniacian to Maastrichtian (Sarjeant 1967a) and now Harker and Sarjeant (1975) give it an ?early Coniacian to ?early Palaeocene range.

Genus SENEGALINIUM Jain and Millepied, 1973

Type species. Senegalinium bicavatum Jain and Millepied, 1973; O.D.

Remarks. The view of Herngreen (1975) on the status of *Senegalinium* is not accepted here. Unfortunately Jain and Millepied (1973) did not stress the mode of archeopyle formation in their original description of *Senegalinium* which is characteristic and unique to this genus, i.e. possessing a large, single plate, elongate hexagonal intercalary archeopyle which almost gives the impression of being precingular.

Senegalinium magnificum (Stanley) comb. nov.

Plate 25, fig. 2

1965 *Deflandrea magnifica* Stanley, pp. 218–219, pl. 20, figs. 1–6.

Figured material. Slide SAL 4383-RH1, specimen MPK 928.

Remarks. This species is herein recombined into *Senegalinium* as it possesses the large intercalary single-plate archeopyle and the small pericoels characteristic of the genus. It was recorded from a single sample in the Montana section. It had a Palaeocene range (Sarjeant 1967a) but Kjellström figured it as *Lejeunia hyalina* from the Maastrichtian (fig. 1 of Kjellström 1972) and this is probably confirmed herein. Zaitzeff and Cross (1970) also have recorded it from the Maastrichtian. Harker and Sarjeant (1975) record the range as early Santonian to early Eocene.

Senegalinium tricuspis (O. Wetzel) comb. nov.

Plate 25, figs. 3, 5

1933b *Peridinium tricuspis* O. Wetzel, 166, pl. 2, fig. 14.

1970 *Astrocysta tricuspis* (O. Wetzel) Davey, p. 360.

1973 *Lejeunia tricuspis* (O. Wetzel) Harland, p. 673, pl. 84, fig. 4.

Figured material. Slides SAL 4380-RH1 and SAL 4381-RH1, specimens MPK 929, 930.

Remarks. This species was observed to possess a large intercalary archeopyle (Pl. 25,

fig. 3) and together with the small pericoels developed in the regions of the apical and antapical horns indicate its affinities to this genus and not to the genus *Astrocysta* Davey whose archeopyle is now known to be transapical (Norris and Hedlund 1972). *S. tricuspis* occurs almost throughout the studied section and indeed Sarjeant (1967a) and Harker and Sarjeant (1975) have recorded a Santonian to Maastrichtian range for the species.

Other species. The following species also belong to this genus: ?*S. albertii* (Corradini, 1972) comb. nov. = *Deflandrea albertii* Corradini, 1972, pp. 174-175, pl. 27, figs. 7a, b, 8; pl. 28, fig. 2. *S. boloniensis* (Riegel, 1974) comb. nov. = *D. boloniensis* Riegel, 1974, pp. 354-356, pl. 1, figs. 6-10; text-figs. 3, 4. *S. gaditanum* (Riegel, 1974) comb. nov. = *D. gaditana* Riegel, 1974, pp. 356-357, pl. 2, figs. 8, 9; pl. 3, figs. 1-2. ?*S. kozlowskii* (Gorka, 1963) comb. nov. = *Lejeunia kozlowskii* Gorka, 1963, p. 41, pl. 5, fig. 4. *S. pannuceum* (Stanley, 1965) comb. nov. = *D. pannucea* Stanley, 1965, p. 220, pl. 22, figs. 1-4, 8-10. *S. pentagonalis* (Corradini, 1972) comb. nov. = *D. pentagonalis* Corradini, 1972, p. 175, pl. 28, fig. 3. ?*S. subquadratum* (Corradini, 1972) comb. nov. = *D. subquadra* Corradini, 1972, pp. 175-176, pl. 28, fig. 1.

GROUP UNCERTAIN

Genus ODONTOCHITINA Deflandre emend. Davey 1970

Type species. *Odontochitina operculata* (O. Wetzel) Deflandre and Cookson, 1955; O.D.

Odontochitina operculata (O. Wetzel) Deflandre and Cookson, 1955

1933a *Ceratium* (*Euceratium*) *operculatum* O. Wetzel, p. 170, pl. 2, figs. 21, 22; text-fig. 2.

1955 *Odontochitina operculata* (O. Wetzel) Deflandre and Cookson, pp. 291-292, pl. 3, figs. 5, 6.

Remarks. This species was found in the lowermost part of the section. Its previously recorded range was Hauterivian to Campanian (Sarjeant 1967a), but McIntyre (1974) recorded it from the ?Maastrichtian, as did Zaitzeff and Cross (1970) but as *O. striatoperforata* (see Williams 1974). Harker and Sarjeant (1975) give this species a range of early Valanginian to late Maastrichtian.

COMPARISON AND INTERPRETATION

The dinoflagellate cyst assemblage recovered from the Bearpaw Formation of Hell Creek, Montana contains a number of forms in common with the same formation in southern Alberta (Harland 1973). These are *Cyclonephelium distinctum* Deflandre and Cookson, *Oligosphaeridium anthophorum* (Cookson and Eisenack) Davey, *O. pulcherrimum* (Deflandre and Cookson) Davey and Williams, *Spiniferites ramosus* (Ehrenberg) Mantell, *Australiella cooksoniae* (Alberti) Vozzhennikova = *Deflandrea korojonensis* Cookson and Eisenack of Harland (1973), *A. tripartita* (Cookson and Eisenack) Vozzhennikova, *D. macrocysta* Cookson and Eisenack, *Diconodinium arcticum* Manum and Cookson, *D. firmum* Harland, *Senegalinium tricuspis* (O. Wetzel) comb. nov., and *Odontochitina operculata* (O. Wetzel) Deflandre and Cookson. Species that are exclusive to the Montana section are *Dictyopyxidia* sp., *Ceratiopsis diebeli* (Alberti) Vozzhennikova, *Deflandrea montanaensis* sp. nov., *D. cf. pirnaensis* Alberti, *Palaeocystodinium golzowense* Alberti, *Palaeoperidinium pyrophorum* (Ehrenberg) Sarjeant, and *S. magnificum* (Stanley) comb. nov. The Montana section contains seventeen species of dinoflagellate cysts as compared to the fifty-three recorded from southern Alberta; eleven species are in common. In

the terms of the categories of relative proportions as given by Harland (1973), *Oligosphaeridium anthophorum*, *A. cooksoniae*, *Ceratiopsis diebeli*, *D. macrocysta*, *D. montanaensis*, *Palaeocystodinium golzowense*, and *S. tricuspis* are 'occasionally common', i.e. making up greater than 10% of the dinoflagellate cyst population on occasions, with the remainder being 'rare'. No species was 'common' throughout the Montana section.

It is now possible to compare the described assemblage with those of Zaitzeff and Cross (1970), Jain and Millepied (1973), Riegel (1974), and McIntyre (1974), especially with regard to *Australiella*, *Diconodinium*, and *Senegalinium*. It is also possible to comment that the present assemblages, together with Harland (1973) and the publications mentioned above, differ from those of Clarke and Verdier (1967) and Wilson (1971), especially with regard to the presence of species belonging to *Diconodinium* and *Senegalinium*. They are comparable, however, in the presence of *Australiella* species and of *Odontochitina operculata*. Some provincialism may be indicated or differences may be caused by local facies or palaeoenvironments. Certainly the northern United States and Canadian assemblages, of this age indicate a single water body during the Late Cretaceous.

A major reason for the differences between the sections and assemblages from southern Alberta and Montana is age. The three species *C. diebeli*, *P. golzowense*, and *S. magnificum* are all much better known from the Maastrichtian than the Campanian, and on plotting the recovered species from the Montana section and including their known stratigraphical ranges in North America (see text-fig. 3) an apparent change in the assemblage occurs at about the level of sample SAL 4380 with no apparent change in the lithology. Here an assemblage with *O. operculata*, *Oligosphaeridium pulcherrimum*, and *Cyclonephelium distinctum* gives way to one containing *Ceratiopsis diebeli*, *P. golzowense*, and *S. magnificum*. Can this be considered as the Campanian-Maastrichtian boundary?

Unfortunately the full results of Wilson's study on the European type Campanian and Maastrichtian stages, preliminarily reported upon in 1971, are not yet published. It would appear, however, that *Odontochitina operculata* has a top at the Campanian-Maastrichtian boundary or just within the earliest Maastrichtian, and that *C. diebeli* is commonly first found in the Maastrichtian (Wilson 1971). There is therefore some evidence for placing the Campanian-Maastrichtian boundary at the level of SAL 4380 and also evidence for regarding the whole section as being Maastrichtian in age. An age assignment of very latest Campanian to Maastrichtian or entirely Maastrichtian may, therefore, be given to the section at Hell Creek in Montana. Evidence from the radiometric data available and the radiometric time scale, as understood at present, appears to support the dinoflagellate biostratigraphy. However, errors are inherent in the construction of such a time scale and the delimitation of absolute time for stage boundaries (see Obradovich and Cobban 1975); but it is interesting that there is some correspondence.

The Bearpaw sea in Montana at this time was probably shallow and under a terrigenous influence, because there is a low proportion of dinoflagellate cysts in the total palynomorph content (only between 1-15% throughout the section), a low species diversity, and a high proportion of peridiniacean to gonyaulacacean cysts (see Harland 1973). This is in contrast to the southern Alberta sections where there

were larger and more diverse populations of dinoflagellate cysts, probably reflecting better palaeoenvironmental conditions. Since the formation in Montana is younger than that in Alberta it is likely to be reflecting the growing influence of continental sedimentation.

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A NEW EOCENE SHARK FROM THE LONDON CLAY OF ESSEX

by H. CAPPETTA and D. J. WARD

ABSTRACT. Teeth of a new scyliorhinid shark *Megascyliorhinus cooperi* gen. nov., sp. nov. from the London Clay are described and compared with *M. miocaenicus* (Antunes and Jonet) a Mio-Pliocene species from France, Portugal, and Tunisia, previously referred to *Rhincodon*. It is suggested that the genus *Megascyliorhinus* inhabited fairly deep water.

RECENT collecting at the London Clay (Eocene) locality of Burnham-on-Crouch, by the junior author (D. J. W.), has produced teeth of a new species of scyliorhinid shark. Independent collecting by the senior author (H. C.) at the Neogene localities of La Motte d'Aigues, France and Nabeul, Tunisia has yielded representatives of the same genus, a species previously only recorded from the Miocene of Portugal.

LOCALITIES

1. Burnham-on-Crouch, Essex. This locality is situated about 3 km WNW. of the town of Burnham-on-Crouch. The London Clay is exposed on the north bank of the River Crouch in a foreshore section from map references TQ 920 968 to TQ 922 966. The formation is a stiff blue-grey clay, weathering to brown, and containing occasional mudstones and septaria. From Whitaker and Thresh (1916, pp. 86–111), it is estimated that the base of the clay is 85 m below high-water mark. The invertebrates are characteristic of Wrigley's divisions 3, 4, and 5 of the London Clay (Wrigley 1924 and 1940). The selachian fauna is identical to that listed from Sheppey (Casier 1966) except for the absence of a few species: *Heterodontus wardenensis* Casier, *Myliobatis latidens* Woodward, and *Aetobatis irregularis* Agassiz. There are in addition several species present at Burnham which are so far unknown from Sheppey: *Triakis* sp., *Mustelus* sp., and *Scyliorhinus* spp.

2. La Motte d'Aigues, France. At this locality, situated at the foot of the south face of Grand Lubéron (Vaucluse), there are three superimposed formations each of which yields a rich selachian fauna. The lower is a marl, the middle a sandstone, and the upper a limestone; the latter yielded a few teeth of *Megascyliorhinus miocaenicus*. These formations are considered as Helvetian *s.l.* in age, probably Serravallian.

3. Nabeul, Tunisia. This locality, about 70 km south-east of Tunis, is a large pit where the blue marls have long been worked by local potters. The selachian teeth come from gypsiferous marls interbedded with the blue marls at the base of the outcrop. These marls are considered to be Early Pliocene in age.

SYSTEMATIC PALAEONTOLOGY

Family SCYLORHINIDAE Gill, 1862

This family is represented in the London Clay by seven species. The teeth of '*Scylorhinus*' *biauriculatus* Casier and '*S.*' *minutissimus* (Winkler) are large, and their inclusion in *Scylorhinus* s.s. is rather doubtful; they somewhat resemble the carcharhinids. *S. gilberti* Casier and three small undescribed species of *Scylorhinus* closely resemble Recent *Scylorhinus* teeth (Cappetta 1976). The new species described below is the largest, the anterior teeth reaching 7.5 mm in height.

Megascylorhinus gen. nov.

Type species. *M. cooperi* sp. nov.

Referred species. *M. miocaenicus* (Antunes and Jonet).

Diagnosis. Scylorhinid known only by isolated teeth; anterior teeth large, curving strongly inwards, lingual face of the crown sometimes striated, labial face particularly convex, smooth or finely striated. The cutting edge, where present, generally does not reach the base of the crown. Root high and broad with flat base and deep median groove; well-developed pair of latero-internal foramina. The lateral teeth asymmetrical, very strongly striated, and may have a pair of lateral denticles.

Megascylorhinus cooperi gen. nov., sp. nov.

Plate 26, figs. 1-3; Plate 27, fig. 1

Derivation of name. This species is dedicated to Mr. J. Cooper in recognition of his work on the London Clay.

Material. Six complete and three fragmentary teeth from Burnham-on-Crouch. Three worn teeth from Sheppey, previously unnoticed among some upper anterior hexanchid teeth in the collection of the B.M. (N.H.). Figured specimens are housed in the B.M. (N.H.), whose registration numbers are quoted.

Holotype. Anterior tooth, P. 57621. Plate 26, fig. 1*a-d*.

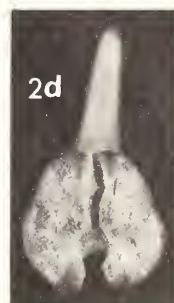
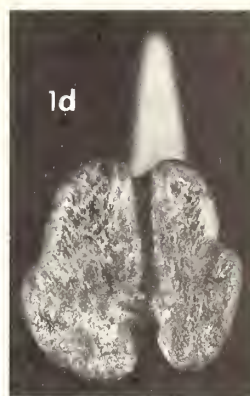
Type locality. Burnham-on-Crouch, Essex, England.

Age. Eocene; Ypresian (London Clay).

Diagnosis. The labial surface of the anterior tooth is inflated towards the bottom of the crown and has short strong parallel striae at its base. The anterior lobes of the root are rounded and outwardly divergent. The root markedly protrudes over the base of the crown in oral view. Extreme lateral teeth have a partially closed root groove.

EXPLANATION OF PLATE 26

Figs. 1-3. *Megascylorhinus cooperi* gen. nov., sp. nov. $\times 10$. Eocene, Burnham-on-Crouch. In each figure, *a*, lingual face; *b*, labial face; *c*, profile; *d*, base. The registration numbers are of the Department of Palaeontology, British Museum (Natural History). 1, anterior tooth. P. 57621. Holotype. 2, anterior tooth. P. 57624. 3, lower lateral tooth. P. 57622.



CAPPETTA and WARD, new Eocene shark

Description. The holotype (Pl. 26, fig. 1) is an anterior tooth with a pointed crown and rather stout base. The crown strongly curves towards the inside of the mouth and is oblique to the root. The inner surface is strongly convex and is ornamented with numerous fine parallel close-spaced striations on its lower quarter. The outer surface is less convex but has a basal swelling protruding over the anterior surface of the root; the area below this swelling is concave and bears short vertical striations, some of which are fairly well spaced. The junction of the root and crown is constricted.

The root is particularly broad and high; the base is flat and the lobes are separated by a deep groove. The internal protuberance is well developed and separated from the general contour by two notches on the prolongation of the latero-internal foramina. These are well developed and occur singly or paired on the lateral face. The inner surface is rather high; the outer surface is very oblique in profile, following the spread of the root towards the anterior lobes, which are rounded and separated by a deep groove. When seen in profile, the enamel junction is straight and slopes up posteriorly. The cutting edge is restricted to the upper third of the crown.

On a slightly larger anterior tooth, the crown is a little less slanting and the base protrudes less over the anterior surface of the root; the cutting edge occupies half the length of the crown.

The lateral teeth are asymmetrical, their crowns being inclined towards the symphysis. On one tooth (Pl. 26, fig. 3), the striations on the outer surface are restricted to the base of the crown, whereas those on the inner surface cover one-half of its height. On the other hand, another tooth (Pl. 27, fig. 1), of similar size and presumed jaw position, shows striations up to two-thirds of the way up the crown, and in addition bears a single well-developed lateral denticle, the other represented by a small protuberance. By comparison with the modern scyliorhinids, this more striated tooth probably belongs to the upper dentition. On both these teeth, the roots are asymmetrical with a more developed lingual lobe; the root groove is oblique, in line with the inclination of the crown.

One very small lateral tooth shows the same characteristics, with less striation, although more strongly defined and covering almost the whole crown; the root groove is partly covered over.

Megascyliorhinus miocaenicus (Antunes and Jonet), 1970

Plate 27, figs. 2-4

1970 *Rhincodon miocaenicus*, Antunes and Jonet, pp. 152-153, fig. 5; pl. 9, figs. 42-44.

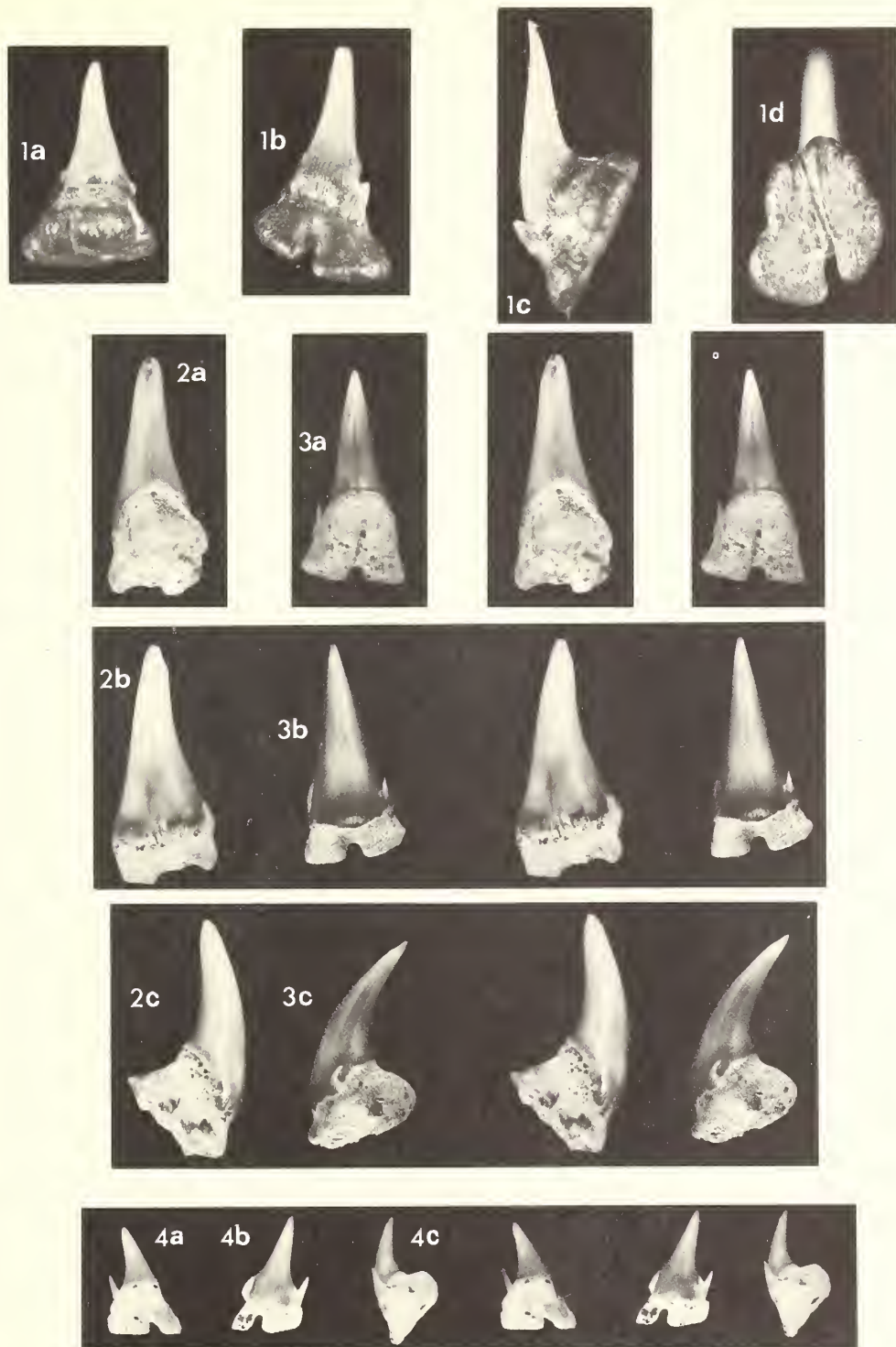
Material. Ten teeth from the Helvetian of La Motte d'Aigues (France) and one tooth from the Pliocene of Nabeul (Tunisia).

EXPLANATION OF PLATE 27

In each figure, *a*, lingual face; *b*, labial face; *c*, profile; *d*, base.

Fig. 1. *Megascyliorhinus cooperi* gen. nov., sp. nov. $\times 10$. Upper lateral tooth. B.M. (N.H.) P. 57623. Eocene. Burnham-on-Crouch.

Figs. 2-4. *Megascyliorhinus miocaenicus* (Antunes and Jonet). $\times 4$. Stereophotographs. The registration numbers are those of the Laboratoire de Paléontologie, Université Montpellier II. 2, anterior tooth. LMA. 1. Helvetian. La Motte d'Aigues. 3, anterior tooth. NAB. 1. Late Pliocene. Nabeul. 4, lateral tooth. LMA. 2. Helvetian. La Motte d'Aigues.



CAPPETTA and WARD, new Eocene shark

Description. (a) Miocene specimens. An anterior tooth (Pl. 27, fig. 2a-c) has a stout crown and no cutting edge. The labial surface of the crown has a few strong striations below its inflated base. The root is damaged, so that only an indication of its size can be given.

A lateral tooth (Pl. 27, fig. 4a-c), lacking a fragment of root, is asymmetrical, its crown being inclined towards the commissure. The lingual surface is very convex; the labial is less so, tending to flatten at the base of the crown. The lingual surface has numerous small wavy striations along its entire height; those of the labial surface are less in number, short in the middle, and longer at the sides. On one side there is a sharp, striated lateral denticle well separated from the main crown; the other is broken. The root is rather high with a strong internal protuberance; its base and outer face are flat, the base is divided by a deep groove.

This lateral tooth is rather different from the anterior teeth, but its general appearance, and in particular its striation and root morphology, favour its inclusion in this species; the presence of denticles on lateral teeth has already been noted in *M. cooperi*.

For a more detailed description of the Miocene species, see Antunes and Jonet (1970).

(b) The Pliocene specimen. This anterior tooth (Pl. 27, fig. 3) is slightly smaller than the Miocene specimens but larger than those from the Ypresian. The crown is stout, and leans less towards the inside of the mouth. There is a single lateral denticle, broad at its base but with a sharp backward-pointing tip. The lower third of the inner surface is striated; the outer surface is smooth. The root is robust, rather high, and has a deep groove at its base.

SYSTEMATIC COMPARISON

One can immediately see the similarities between the Eocene and Mio-Pliocene species, and there can be little doubt that they are directly related. Their appearance is similar, but there are sufficient small differences to separate them. The teeth of the Eocene species have a longer crown, which is more inclined towards the inside of the mouth, with many well-defined striations at the base of the outer surface. The root is lower and slightly different in shape: the front is rather oblique and the lobes are quite large. This Ypresian species is quite easy to separate from the other Eocene scyliorhinids, in particular by its combination of large size, striations, and the absence of lateral denticles on the anterior teeth.

The teeth of *M. miocaenicus* are stouter. Their crowns lean less towards the inside of the mouth, the striations at the base of the outer surface are less developed, the root is higher, and the outer surface is subvertical.

The Neogene species cannot be mistaken for any other scyliorhinid. Only the lateral teeth approach those of *Scyliorhinus distans* (Probst), and they can be easily separated by their stouter crown, finer and more numerous striations, the shape of the root, and the more jagged outline of crown and denticles. The Mio-Pliocene teeth agree with those from the Tortonian of Portugal figured by Antunes and Jonet (1970, p. 153, fig. 5 and pl. 9, figs. 42-44) under the name *Rhincodon miocaenicus*; they are anterior teeth without lateral denticles. Antunes and Jonet place in the

synonymy of *R. miocaenicus* the tooth figured in Cappetta (1970) under the name *Rhincodon* sp. from the Helvetian of Loupian, Languedoc, France. Antunes and Jonet state: 'les caractères morphologiques de la racine de ces dents (i.e. *R. miocaenicus*) semblent identiques à ceux de la dent décrite par Cappetta (i.e. *Rhincodon* sp.) mais il y a quelques différences en ce qui concerne la couronne.'

However, these differences are extremely important, particularly in the region of the root. We have examined the teeth of a specimen of the modern whale shark, *R. typus* Smith, from the Seychelles: these teeth are characterized by their small size, by a smooth erect crown with a distinct cutting edge, and by a wide rounded enamel lingual apron, which in profile reaches the base of the root. The root is high, elongated labio-lingually, with a large internal protuberance and a deep groove; the sides are very swollen and the latero-internal foramina are particularly close to the lingual surface. The Loupian tooth corresponds completely with the modern teeth and certainly represents a true *Rhincodon* and not an upper tooth of *M. miocaenicus* as supposed by Antunes and Jonet (1970, p. 154). These authors were probably misled by the figure of a tooth of *R. typus* in Bigelow and Schroeder (1948, p. 190). This illustration is inaccurate because it shows a tooth without its lingual apron, an important feature present in all the teeth we have been able to study, but absent in *M. miocaenicus*. In 1930 White had already, correctly, figured a *Rhincodon* tooth (p. 143, fig. 9). As the species *miocaenicus* does not belong to the genus *Rhincodon*, but instead closely resembles the species *M. cooperi*, it is therefore placed in that new genus. *Megascyliorhinus* is included in the Scyliorhinidae because of its broad similarity with other members of the family, particularly *Scyliorhinus s.s.*; nevertheless, this genus differs from all the genera of the family that we have examined.

STRATIGRAPHIC DISTRIBUTION

Megascyliorhinus first appears in Divisions 3–5 of the London Clay (Ypresian) at Burnham-on-Crouch and Sheppey, England. The tooth described by Brzobohaty and Kalabis (1970, pl. 2, fig. 2a–b) from the Oligocene of Pouzdrany, Czechoslovakia, and referred by those authors to *Odontaspis*? sp., is very suggestive of this genus. This anterior tooth shows all the characteristics of the genus. Its crown is typically stocky and inclined, resembling the Eocene species more closely than the Mio-Pliocene one. It can be distinguished from those of the Eocene species by the less prominent anterior lobes of the root and by the presence of a pair of lateral denticles; this feature occasionally appears on anterior teeth, as seen in the Pliocene specimen. The genus is not known again until the Helvetian *s.l.* of La Motte d'Aigues, France where it is represented by *M. miocaenicus*, and again in the Tortonian VII at Mutela in Portugal. The most recent specimen is from the Early Pliocene of Nabeul in Tunisia. This genus probably became extinct in the Pliocene or Pleistocene.

PALAEOECOLOGY

The base of Wrigley's London Clay Division 2 and the base of the Aldwick Beds at Bognor Regis, Sussex mark the influx of a number of shark species which make their first appearance in the English Eocene. These include a few species rare or absent

in contemporary shallow-water deposits in the Paris-Belgian Basin, for example *Notorhynchus serratissimus* (Agassiz), *Xenodolamia eocaena* (Woodward), and *Anomotodon sheppeyensis* (Casier) [= *Oxyrhina sheppeyensis* Casier], all presumed to be deep-water species. In the Miocene, *Megascyliorhinus* is associated with *Deania*, *Centrophorus*, *Pristiophorus*, and *Raja*. Living species of these genera, with perhaps the exception of *Raja*, prefer deep water. At La Motte d'Aigues, where there is a series of closely similar faunas in the Helvetian, *Megascyliorhinus* is restricted to limestone facies at the top, and is absent from the lower marly and sandy facies. In Tunisia, the sole tooth was collected from gypsiferous marls at the base of blue marls rich in otoliths of Myctophidae, which are deep-water fishes. The nature of these deposits and their faunal associations suggest that *Megascyliorhinus* inhabited depths of around 150–200 m.

Acknowledgements. We would like to thank Dr. C. Patterson, Messrs. J. Cooper and J. Hooker of the B.M. (N.H.) for reading and criticizing the manuscript. The photographs of *M. cooperi* were by Mr. P. York and those of *M. miocaenicus* by Monsieur J. Martin. Mrs. J. Powell assisted in the translation of the French draft and the English manuscript was typed by Mrs. D. Ward.

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THE GIANT CROCODYLIAN *SARCOSUCHUS* IN THE EARLY CRETACEOUS OF BRAZIL AND NIGER

by E. BUFFETAUT and P. TAQUET

ABSTRACT. Re-examination of crocodilian remains previously referred to *Goniopholis*, from the lower Cretaceous of the Bahia basin (Brazil), shows they really belong to the genus *Sarcosuchus* (Mesosuchia, Pholidosauridae), formerly known from the Aptian of the Sahara. Resemblances between early Cretaceous African and South American vertebrate faunas anterior to the opening of the South Atlantic Ocean are stressed.

IN 1966 de Broin and Taquet announced the discovery of a new giant crocodilian, *Sarcosuchus imperator* (suborder Mesosuchia, family Pholidosauridae), in early Cretaceous continental strata of Algeria and Niger. Since then, abundant material has been collected at the Gadoufaoua locality, in the Tegama basin of Niger (Taquet 1970); it includes complete skulls and skeletons, and provides much new information on the anatomy of this African form. On the other hand, a re-examination, by E. Buffetaut, of crocodilian remains found at the turn of the century in the early Cretaceous Bahia series of the Recôncavo (or Bahia) basin, on the north-eastern coast of Brazil, shows that the successive attributions given to these fossils by various authors are erroneous. A comparison between the specimens from Brazil and those from Niger leads us to attribute the remains from Bahia to the genus *Sarcosuchus*, and to stress the similarities between the early Cretaceous African and South American continental faunas.

As early as 1860, vertebrate remains from the Recôncavo basin, among which were two different types of crocodilian teeth, were described by Allport. In 1869 Marsh erected two new species for a few isolated teeth found by Hartt in the same area: *Crocodylus hartti*, with large, finely wrinkled teeth, and *Thoracosaurus bahiensis*, with smaller, coarsely striated teeth. Later, Woodward (1888) referred other scanty remains to *Hyposaurus derbianus*, a species described by Cope (1886) from the Late Cretaceous of Pernambuco. More important material, discovered by Mawson, was also studied by Woodward (Mawson and Woodward 1907), who then attributed all crocodilian remains from the Bahia formation to the genus *Goniopholis*, with two species, *G. hartti* (Marsh, 1869)—which included all the newly discovered fossils—and *G. bahiensis* (Marsh, 1869). The remains of '*Goniopholis hartti*', now in the British Museum (Natural History), which have been subjected to a re-examination, comprise the anterior part of a large lower jaw (R 3423), a dorsal scute (R 3224), and two teeth (R 2983, R 3079).

Similarities between these fossils and *S. imperator* are numerous (Pl. 28). In both instances, the very long mandibular symphysis is indicative of a long-snouted animal (Pl. 28, figs. 1, 2), while in the short-snouted genus *Goniopholis* the symphysis is always short. Other remarkable resemblances between the Brazilian form and

S. imperator include the spatulate shape of the anterior extremity of the mandible, the relative size of the alveoli (with small first and second, and enlarged third and fourth alveoli), and the coarse ornamentation of the ventral surface of the bone. The scute found in Brazil (Pl. 28, fig. 5) is very similar to some dorsal plates of *S. imperator* (Pl. 28, fig. 4), which have the same general outline, likewise bear an antero-external 'peg', and possess a smooth anterior rim (which was overlapped by the preceding scute). The presence of a peg on the dorsal scutes is by no means restricted to *Goniopholis*, but occurs in several other crocodilian genera, such as the Jurassic teleosaurid *Steneosaurus*, as already mentioned by Woodward in a footnote to the 1907 article. The large teeth of the animal from Bahia are also very reminiscent of *Sarcosuchus imperator*, in their stout general shape and in the ornamentation of their enamel, consisting of fine sinuous wrinkles. Lastly, both the African and the South American forms are very large. *S. imperator* is one of the largest known crocodilians, with a skull up to 170 cm in length, and an estimated over-all length of 11 m. The jaw fragment from the Recôncavo basin is 43 cm long, although it is only the anterior part of the symphysis.

Thus, Woodward's attribution of the Brazilian fossils to *Goniopholis*, which was based mainly on the presence of a peg on the dorsal scute, cannot be considered as valid. In our opinion, this South American crocodilian belongs to the genus *Sarcosuchus*. In the absence of more complete material from South America, it seems acceptable to retain different specific names for the African and the South American forms, and to call the latter *S. hartti* (Marsh, 1869). However, the differences between the two forms (in the spacing of the alveoli, for instance) seem rather unimportant, so that the possibility that they may belong to the same species cannot be excluded.

There may well be crocodilians other than *S. hartti* in the Bahia series, but they are represented by very scanty remains, which do not allow a precise identification. Although Roxo (1936) tried to revalidate *T. bahiensis* on the basis of a tooth and a procoelous vertebra of uncertain origin, the occurrence of the essentially marine late Cretaceous genus *Thoracosaurus* in the early Cretaceous freshwater Bahia series is most unlikely, as already pointed out by Antunes (1964). There is also no serious reason to assume that *H. derbianus* occurs in the Early Cretaceous of the Recôncavo basin. Both identifications were made in the erroneous belief that the Bahia series was of late Cretaceous age.

Besides crocodilian remains, the fossil material from the Recôncavo basin includes the centrum of a dorsal vertebra of a carnosaur (Allport 1860), too incomplete to be compared with the vertebrae of the several carnosaurs known from Niger. Woodward (Mawson and Woodward 1907) also mentions vertebral centra which 'seem

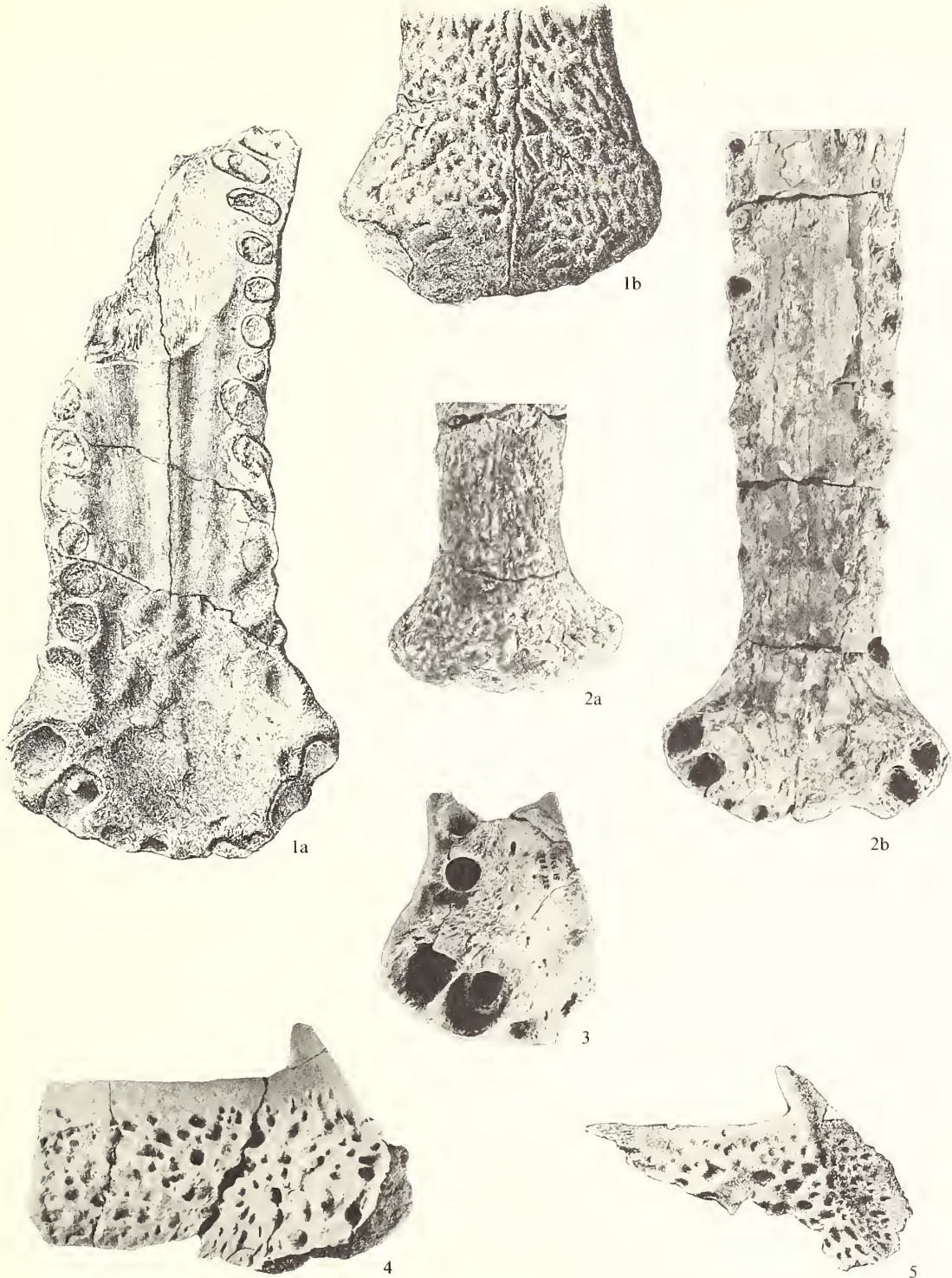
EXPLANATION OF PLATE 28

Sarcosuchus remains from Brazil and Niger, $\times 0.25$.

Fig. 1. *Sarcosuchus hartti*, from Brazil, B.M.(N.H.) Specimen No. R 3423; anterior extremity of lower jaw (from Mawson and Woodward 1907); a, in dorsal view; b, in ventral view.

Figs. 2-4. *Sarcosuchus imperator*, from Niger. 2, anterior extremity of lower jaw of young individual; a, in ventral view; b, in dorsal view. The very spatulate shape is due to the youth of the animal. 3, anterior extremity of right dentary of adult specimen, in dorsal view. 4, dorsal scute.

Fig. 5. *Sarcosuchus hartti*, from Brazil: dorsal scute (from Mawson and Woodward 1907).



BUFFETAUT and TAQUET, Giant crocodilian from Brazil and Niger

to agree closely with the corresponding bones of Iguanodonts'; this information, if true, is interesting, since several iguanodontids are known from the Early Cretaceous of Niger (Taquet 1970). The vertebrate fauna from Bahia also includes scales of the holostean fish *Lepidotus* (with three species) and remains of two species of the coelacanth *Mawsonia* (Patterson 1975). The genus *Lepidotus* is also represented in the Tegama basin of Niger by numerous skull remains and large scales (now being studied), while a skull and several post-cranial fragments of a *Mawsonia* from the same area will soon be described by Wenz. Patterson (1975) has stressed the resemblances between the early Cretaceous fish faunas from the Recôncavo and Gabon basins. We can now parallelize the freshwater faunas from these regions with the one from the Tegama basin (Table 1), and include *Sarcosuchus* in the list of early Cretaceous genera common to South America and to Africa.

TABLE 1. Comparative list of early Cretaceous vertebrate genera common to South America and Africa.

Recôncavo basin (Bahia series)	Gabon basin (Cocobeach series)	Tegama basin (Aptian)
<i>Mawsonia major</i>	Coelacanth	<i>Mawsonia</i> (new species)
<i>M. minor</i>		
<i>Lepidotus mawsoni</i>	<i>Lepidotus</i> sp.	<i>Lepidotus</i> sp.
<i>L. souzai</i>		
<i>L. roxoi</i>		
<i>Sarcosuchus hartti</i>		<i>Sarcosuchus imperator</i>

The Recôncavo basin is a 'semi-graben' (Fonseca 1966) which was filled, during the early Cretaceous, by the several thousand metres of freshwater sediments of the Bahia series, consisting mainly in conglomerates, shales, and sandstones. Both the lithology and the fauna of this so-called 'Gondwana Wealden' (Krömmelbein 1966) are indicative of a 'shallow lacustrine environment' (Fonseca 1966). As pointed out by Beurlen (1961), these sediments can hardly have accumulated in geographical conditions similar to the present ones, i.e. a basin open on the Atlantic Ocean. The eastern part of the graben is to be found on the West coast of Africa (text-fig. 1),



TEXT-FIG. 1. Map showing the three basins mentioned in the text: 1, Recôncavo (or Bahia) basin, Brazil. 2, Gabon basin, Gabon. 3, Tegama basin, Niger. (After Martin (1968), modified.)

where the Gabon basin exhibits a succession of freshwater deposits (the Cocobeach series) very similar to the Bahia series (de Klasz 1965). The study of ostracod faunas from both areas shows that, according to Krömmelbein (1966), 'it seems that these ostracods lived in one single basin with completely free interchange'; this has allowed a detailed stratigraphical correspondence to be established (Krömmelbein 1971). The end of lacustrine sedimentation in the Recôncavo-Gabon graben is indicated by salt deposits of Aptian age (Reyment 1973). According to Mawson's (Mawson and Woodward 1907) and Fonseca's (1966) maps, the remains of *S. hartti* were collected in the Ilhas Formation, which belongs to the upper part of the Bahia series; they are thus probably a little older than the Aptian. *S. imperator*, from the Tegama basin, is of Aptian age. Therefore, the chronological gap between the two species is probably not very great.

The formation of the Recôncavo-Gabon graben, and of others of the same kind (Potiguar, Sergipe-Alagoas) at the beginning of the Cretaceous, is considered as an early stage in the separation between Africa and South America (Reyment and Tait 1972). The presence of the non-marine crocodilian *Sarcosuchus* in both Brazil and Niger affords additional evidence of the faunal continuity between these continents during the early Cretaceous, before the complete opening of the South Atlantic Ocean.

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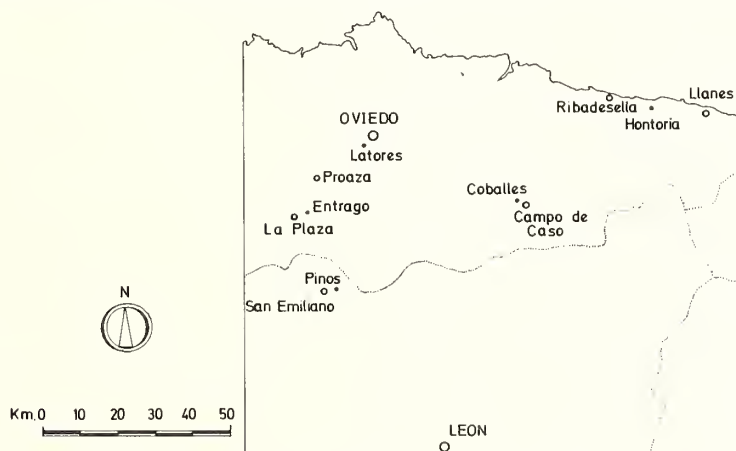
Typescript received 19 December 1975

NEW CARBONIFEROUS STENOSCISMATACEAN BRACHIOPODS FROM OVIEDO AND LEON, SPAIN

by M. L. MARTINEZ-CHACON

ABSTRACT. Four new species of Stenoscismatacea, *Camerisma* (*Callaiapsida*) *alcaldei*, *C. (Callaiapsida)* *paucicostata*, *Cyrolexis granti*, and *Stenoscisma winkleri* are described from the Cantabrian Mountains. The two species of *Callaiapsida*, from the lower and upper Bashkirian, are the oldest attributed to the subgenus, and they show transitional characters between *C. (Camerisma)* and typical *C. (Callaiapsida)*; moreover, the distribution of the subgenus is now extended from the Arctic. *Cyrolexis granti* from the Kashirian is also the oldest species of the genus, previously known only from the Permian.

THE Carboniferous Rhynchonellida from the Cantabrian Mountains are little known; they are infrequently cited and only two authors, Mallada (1875) and Delépine (1943), have described Carboniferous species belonging to the order. Moreover, the majority of these citations and descriptions refer to the Rhynchonellacea and until now only two forms of the superfamily Stenoscismatacea are known in the region: *Camarophoria crumena* (Martin) described by Mallada (1875) from different points in Palencia and *Coledium* sp. quoted by Wagner (1971b, Winkler Prins's determination) also from Palencia province. The present paper constitutes a first attempt to attain a regional knowledge of the representatives of this interesting group. Four new species are described, belonging to *Camerisma*, *Cyrolexis*, and *Stenoscisma*. They come from Oviedo and Leon, provinces very different from Palencia, despite all three being in the Cantabrian Mountains. Text-fig. 1 shows



TEXT-FIG. 1. Map showing the situation of the fossiliferous localities.
.... provincial boundary.

U. S. S. R.		W. EUROPE	Entrago - Pinos area	Latorres area	C. de Caso-Coballes area	Hontoria area
MOSCOWIAN	PODOLSKIAN	C			Escalada Fm.	Escalada Fm.
	KASHIRIAN	B			Beleño Fm.	Shales and sandstones
	VEREYAN	A	San Emiliano Fm.			
BASHKIRIAN	UPPER	NAMURIAN	Valdeteja Fm.	Valdeteja Fm.	Valdeteja Fm.	
	MIDDLE					
	LOWER					
NAMURIAN		C				

TEXT-FIG. 2. Chart of the Carboniferous formations in the area, showing correlation with the Western European and Russian standard sections.

the situation of the fossiliferous localities and text-fig. 2 shows the lithostratigraphical units in the area and their age. All the specimens are housed in the Departamento de Paleontología de la Universidad de Oviedo.

SYSTEMATIC DESCRIPTIONS

Superfamily STENOSCISMATACEA Oehlert, 1887

Family ATRIBONIIDAE Grant, 1965

Subfamily ATRIBONIINAE Grant, 1965

Genus CAMERISMA Grant, 1965

1965a *Camerisma* Grant, p. 63.

1971 *Camerisma* Grant; Grant, p. 323.

Type species. *C. prava* Grant, 1965.

Subgenus CALLAIAPSIDA Grant, 1971

1971 *Camerisma (Callaiapsida)* Grant, p. 323.

Type species. *C. (Callaiapsida) kekuensis* Grant, 1971.

Discussion. The Cantabrian specimens are smaller-sized than typical *C. (Callaiapsida)*; they show the characteristic peripheral grooves of the subgenus but with a much smaller development than those of the type species and of *C. (C.) arctica* (Holtedah, 1924) in Grant's (1971) figures; in addition, one of the forms here assigned to the subgenus bears ribs on the anterior part of the flanks. The internal characters coincide with those of *Callaiapsida* since the space between the camarophorium and the hinge plate is filled by secondary shell covering the intercamarophoral plate. On the basis of the peripheral grooves and internal characters these

species of *Camerisma* are assigned to the subgenus *Callaiapsida*, in spite of the short development of the grooves and small size of both forms, and the ribbed flanks of one of them. *Camerisma* (*Callaiapsida*) has been recorded from Podolskian and Permian rocks. The species here described, of lower and upper Bashkirian age, are the oldest yet recorded. It could be supposed that *C.* (*Callaiapsida*) would evolve in time from *C.* (*Camerisma*), with larger size and greater development of peripheral grooves; perhaps the Cantabrian species are the link between both subgenera. On the other hand, Grant (1971) suggests that *C.* (*Callaiapsida*) is exclusively Arctic in its distribution; this may be correct for the Permian, but during the Carboniferous the subgenus was more widely distributed, since it is unlikely that Northern Spain was at such high latitudes in the Carboniferous.

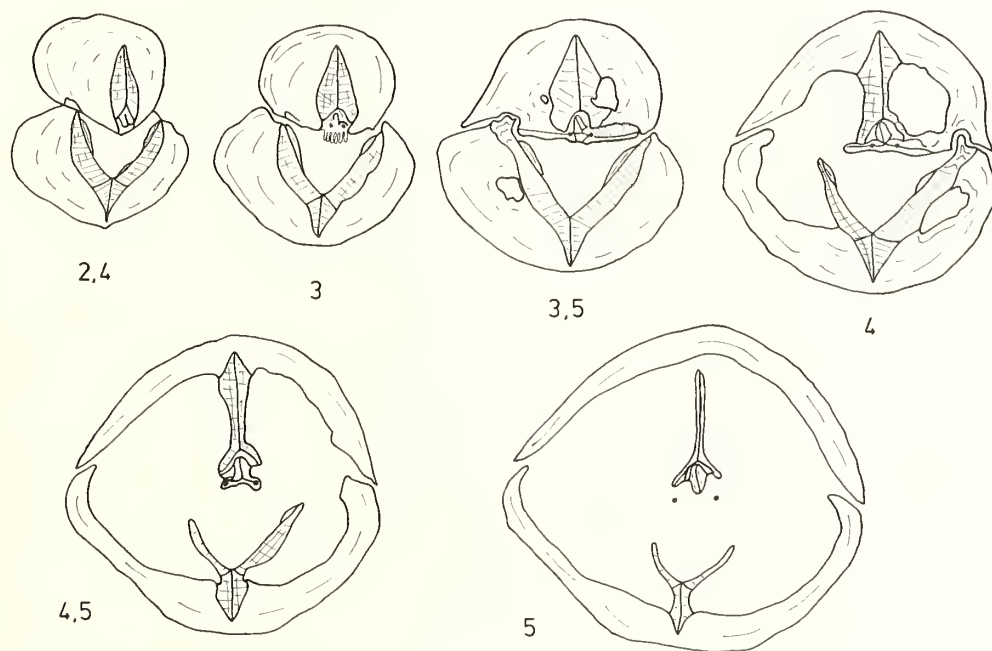
Camerisma (*Callaiapsida*) *alcaldei* sp. nov.

Plate 29, figs. 1-7; text-fig. 3

Derivation of name. Dedicated to Dr. J. L. García-Alcalde.

Material. Holotype (DPO 6915, Pl. 29, figs. 1-5), 13 paratypes (DPO 6916-6928) and other 42 specimens (DPO 6929-6970) from the type locality and 11 specimens (DPO 6971-6981) from Entrago (Oviedo).

Type horizon. A light grey limestone, containing many brachiopods, crinoids, bryozoans, and molluscs, from the upper part of the Valdeteja Formation, of Lower Bashkirian age, from Latores village (6 km SW. of Oviedo), at the top of a small hill, 222 m high, near the km 7 of the Vasco-Asturiano railroad. Latitude 43° 19' 55", longitude 2° 12' 15".



TEXT-FIG. 3. *Camerisma* (*Callaiapsida*) *alcaldei* sp. nov. Transverse sections of specimen DPO 6928 showing internal structures of both valves, especially the development of spondylium and camarophorium. Distances from the ventral beak in mm, $\times 4$.

Diagnosis. Species small for the subgenus, with very high and keel-shaped dorsal median fold, incipient peripheral grooves and smooth flanks.

Description. Small shell of trigonal outline and keel-shaped profile; slightly transverse (L/W average of 0,84), although elongated in young stages; with anteriorly spreading flanks; rather thick (L/T average of 1,31); dorsibiconvex; anterior commissure strongly uniplicate with inverted V-shape; shell frequently somewhat asymmetrical. Ventral valve gently convex. Beak pointed and strongly curved over dorsal umbo, without pedicle foramen. Sulcus beginning near middle of valve as a shallow and wide depression with rounded floor, widening and deepening rapidly toward the front, where it strongly curves dorsally to join the opposite fold through a high tongue; sulcus with median groove becoming stronger anteriorly. Ventral flanges appear anterior to articulation zone, overlapped by dorsal ones and giving way anteriorly to narrow and shallow peripheral grooves, covered by a very thin extension of valve edge (see Pl. 29, figs. 4, 6, 7). Dorsal valve strongly convex, with a beak pointed, directed towards ventral valve and covered by it; umbonal region very convex and high. A sharp and keel-shaped fold starts in posterior half of valve; separated from flanks by two more or less pronounced grooves ending at boundary between anterior and lateral commissures; flanks descending also abruptly (although to smaller degree than fold) from such grooves to the commissure. Dorsal flanges overlapping ventral ones all around commissure, with greatest overlap in posterior part.

Ornament only of growth lines, more visible on ventral valve, especially on the ventral flanks.

Dimensions of some specimens in mm

DPO	L	W	T	DPO	L	W	T
6915	15	20,8	14,8	6923	16,3	17,5	12,6
6916	15,8	19,3	14,4	6924	15,4	19,1	13,3
6917	15,4	20,5	12,5	6925	19	20,5	11,7
6918	13,1	15,6	10,5	6926	9,9	9,2	5
6919	15,9	17,1	9,6	6927	14,6	15,6	9,3
6920	16,6	19,5	14,8	6971	12,4	18,2	11,2
6921	13,1	15	10	6972	13,9	18	13,6
6922	12,1	14,5	8,8				

EXPLANATION OF PLATE 29

Figs. 1-7. *Camerisma (Callaiapsida) alcaldei* sp. nov., $\times 2$. 1-5, holotype, DPO 6915. 1-3, dorsal, ventral, and lateral views. 4, anterior view showing incipient peripheral groove on tongue covered by very thin extension of ventral valve margin. 5, posterior view showing peripheral groove on the left lower side and spondylium. 6, 7, anterior view of paratypes, DPO 6916, 6917, both showing incipient peripheral grooves on tongue.

Figs. 8-12. *Camerisma (Callaiapsida) paucicostata* sp. nov., $\times 2$. Holotype, DPO 6982, dorsal, ventral, lateral, anterior, and posterior views showing pronounced asymmetry; note poorly developed peripheral groove on tongue in fig. 11.

Figs. 13, 14. *Stenosisma winkleri* sp. nov., $\times 3$. DPO 7273, 7272, posterior view of two internal moulds of both valves showing spondylium and camarophorium.

Fig. 15. *Cyrolexis granti* sp. nov., $\times 4$. Holotype, DPO 7283, posterior view of a specimen with valves partially destroyed, showing part of spondylium and camarophorium.



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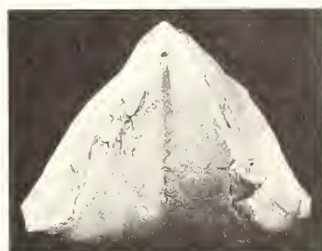
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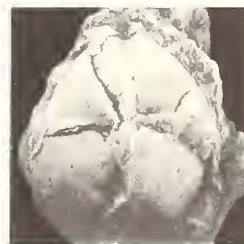
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Ventral interior posteriorly very thickened, spondylium large (see text-fig. 3), with thick walls, supported by low and broad median septum duplex, buried by secondary shell in posterior part (and further forward) so as to appear sessile in its beginning; septum continuing slightly forward of the spondylium. Teeth strong, short, rounded, and each one presenting a lateral exterior crenulation. Dorsal interior also posteriorly thickened. Camarophorium with high and slender median septum duplex, supporting narrow trough with semicircular transverse section. Thick and duplex intercamarophorial plate buried posteriorly in secondary shell, free anteriorly when it ceases to support the hinge plate. Short hinge plate finishing behind camarophorium; inner hinge plates extending more anteriorly than outer hinge plates. Big, rounded cardinal process, with myophore of high lamellae. Crura diverging from hinge plate anteroventrally. One specimen, with part of its anterior flank decorticated, shows deep pallial impressions which branch dichotomously, especially close to the anterior margin.

Discussion. *C. (C.) alcaldei* is distinguished from typical *Callaiapsida* by its smaller size and poorly developed peripheral grooves. Its general form looks like *Camerisma (Camerisma) sella* (Kutorga, 1844) and *C. (Callaiapsida) paucicostata* sp. nov., but the difference between them is the presence of a higher and narrower fold and the absence of ribs on the flanks in the former.

Camerisma (Callaiapsida) paucicostata sp. nov.

Plate 29, figs. 8–12; text-figs. 4, 5

Material. Holotype (DPO 6982, Pl. 29, figs. 8–12), 6 paratypes (DPO 6983–6988) and 12 other specimens (DPO 6989–7000) from the type locality (locality 30 of Winkler Prins, 1968) and 2 other specimens (DPO 7001, 7002) from a nearby locality (locality 29 of Winkler Prins, 1968).

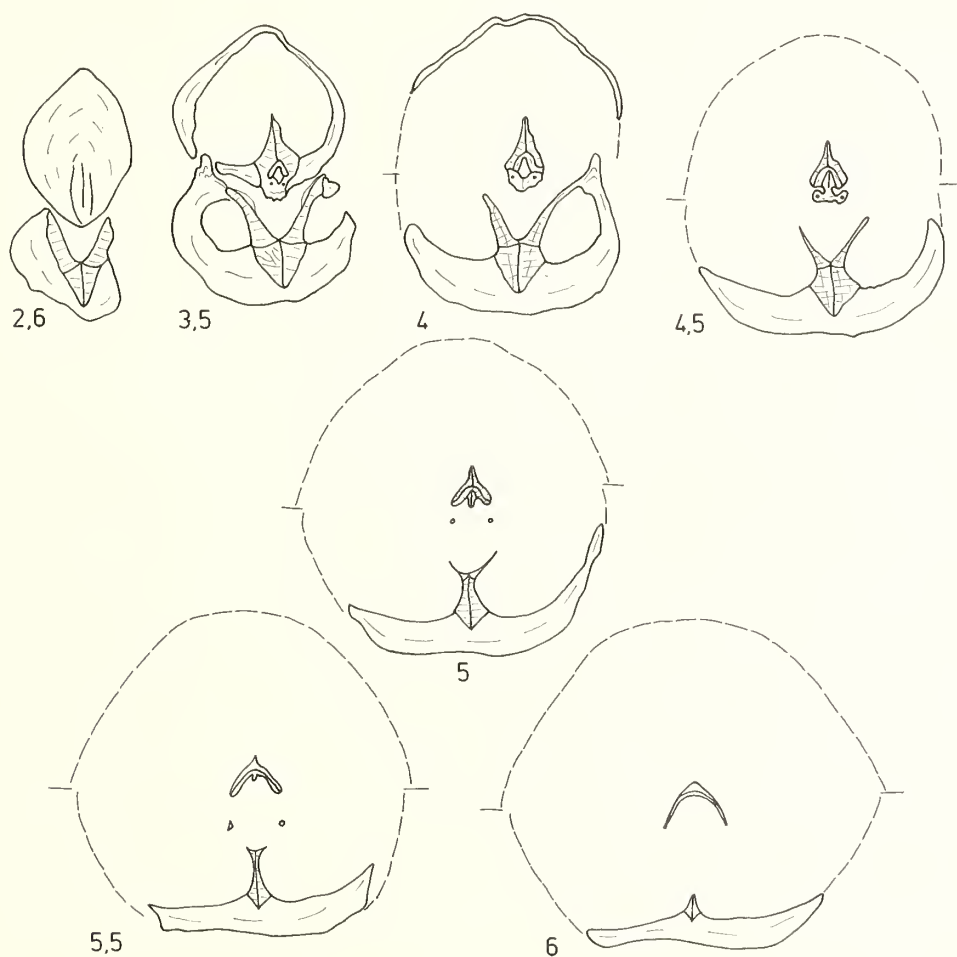
Type horizon. A limestone in the upper part of the San Emiliano Formation, Upper Bashkirian age, north-east of Pinos village (León), slope of the mount on the left from Pinos following the Alcantarilla stream. Latitude 42° 59' 11", longitude 2° 16' 56".

Diagnosis. Small for the subgenus, with high and keel-shaped fold, flanks ornamented by one to three ribs, peripheral grooves with slight development and rather pronounced asymmetry.

Description. Small shell of trigonal outline and keel-shaped profile, transverse (L/W approximately 0,75), rather thick (L/T approximately 1,15), with anteriorly spreading flanks; dorsibiconvex; anterior commissure strongly uniplicate and inverted V-shaped; pronounced asymmetry. Ventral valve gently convex. Beak pointed and strongly incurved over dorsal umbo, without pedicle opening. Sulcus beginning near posterior third of valve as gentle and rounded depression deepening anteriorly, where it curves dorsally into the high V-shaped tongue; median groove running along floor and commonly asymmetrical anteriorly; sulcus separated from each flank by one rib. Flank towards which median groove slopes is less well developed. Ventral flanges posteriorly overlapped by dorsal ones, anteriorly giving rise to shallower peripheral grooves, which are covered by a laminar expansion of valve edge (see text-fig. 5 and Pl. 29, fig. 11). Dorsal valve very convex in transverse section. Beak ventrally directed, sinking in other valve and covered by opposite beak. Umbo very

convex and high. Median fold starting in posterior third of valve, keel-shaped, posteriorly narrow but widening anteriorly, bordered by grooves separating it from steep flanks. As in the ventral valve, one flank, commonly better developed. Dorsal flanges with greatest overlap posteriorly. Flanks ornamented by one to three strong, angular ribs on each one, those bordering the fold and sulcus developed first, the lateral ribs only formed near the anterior margins. Ribs more prominent on ventral valves and more numerous on the larger side of shells. Growth lines faint except on the tongue where they may be almost rugose.

Ventral interior with spondylium supported by low and thick median septum duplex (see text-fig. 4), buried by secondary shell posteriorly so as to appear sessile; when septum is conspicuous, its base is very thickened, thickness decreasing anteriorly and dorsally; spondylium rather narrow ventrally, widening dorsally. Teeth

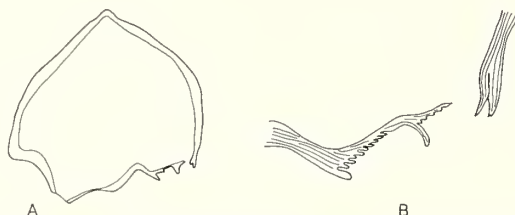


TEXT-FIG. 4. *Camerisma (Callaiapsida) paucicostata* sp. nov. Transverse sections of specimen DPO 6988 showing internal structures. Distances from the ventral beak in mm, $\times 4$.

are short, rounded, and weak. Dorsal interior posteriorly thickened to bury the high but short median septum duplex supporting a short narrow trough of the camarophorium. Intercamarophorial plate buried posteriorly. Hinge plate with very wide and short outer hinge plates and very narrow and rather long inner ones, which cover the camarophorium only posteriorly. Cardinal process large and rounded, with its myophore of short lamellae. Crura project forward from the hinge plate ventrolaterally.

*Dimensions of some specimens
in mm*

DPO	L	W	T
6982	15,3	19	13,2
6984	14,1	19,2	—
6985	16	21,7	14
6986	—	21,2	16
6987	17	21,8	14,6



TEXT-FIG. 5. *Camerisma (Callaiapsida) paucicostata* sp. nov. A, transverse section near the front of deformed specimen DPO 6983 showing incipient peripheral groove on the right, $\times 3$. B, detail of the same section, with poorly developed groove, $\times 13$.

Discussion. *C. (Callaiapsida) paucicostata* and *C. (Callaiapsida) alcaldei* are smaller and have less well developed peripheral grooves than the type species of *Callaiapsida*. *Camerisma (C.) paucicostata* is distinguished from the other Cantabrian species by its ribbed flanks, lesser thickness (owing to a lower fold) and greater degree of asymmetry. It resembles *C. (Camerisma) sella* (Kutorga), as figured by Tschernyschew (1902, pl. 23, fig. 4), in its general form and ribbed flanks; however, on the figures the peripheral grooves are not apparent and are not mentioned in the description. Grant (1971) assigned the species to *C. (Camerisma)*, so he too must have considered the peripheral grooves to be lacking. On the other hand, *paucicostata* seems to have more and better-developed ribs, in contrast to *C. (C.) sella* where they are more evident on the dorsal valve than on the ventral. *C. (C.) sella* is a little larger than *C. (Callaiapsida) paucicostata*, with the maximum width more posteriorly located and it presents a lower asymmetry level.

Subfamily PSILOCAMARINAE Grant, 1965
Genus CYROLEXIS Grant, 1965

1965a *Cyrolexis* Grant, p. 88.

Type species. Cyrolexis haquei Grant, 1965.

Cyrolexis granti sp. nov.

Plate 29, fig. 15; Plate 30, figs. 23–26

Derivation of name. Dedicated to Dr. R. E. Grant.

Material. Holotype (DPO 7283, Pl. 29, fig. 15), specimen with the two valves partially destroyed showing part of the internal structures, and twenty paratypes (DPO 7284–7302, 8522) from the type locality and six specimens (DPO 7303–7307) from three nearby localities. All the specimens are preserved as moulds or casts, except for the holotype in which some shell remains.

Type locality. Basal part of a blackish shale, thickness of 25–30 m, in the upper part of the Beleño Formation, about 80 m below the Escalada Formation (Lower Moscovian, probably Kashirian, according to Winkler Prins, 1968), between Campo de Caso and Coballes (Oviedo), on the right of the road from Riaño to Oviedo, coming from km 53 to 54. Longitude $1^{\circ} 39' 50''$, latitude $43^{\circ} 10' 47''$.

Diagnosis. Small, globose and transverse shell with a fold weakly differentiated from the flanks, and beginning in posterior half of valve; bearing two strong ribs. Sulcus shallower than fold, beginning generally anteriorly to it and having a median rib, flanks smooth or with a rib. Interior with no intercamarophorial plate or developed only as a low elevation on the posterior floor of the camarophorium; hinge plate supported by sides of posterior part of camarophorium.

Description. Small (length between 5 and 7 mm), transverse (width between 7 and 9 mm), globose and dorsibiconvex shell. Anterior commissure sulcificate. Ventral valve with greatest convexity in umbonal region; beak short and slightly incurved over dorsal one. Sulcus shallow, with rounded floor and greatly widening anteriorly; at about 3 mm or more forward from the umbo a wide but low and rounded rib developed. In some specimens a pair of ribs separate the sulcus from the flanks. Posteriorly flat flanges are overlapped by those of the dorsal valve. Dorsal valve more strongly convex; beak short, ventrally directed and covered by that of opposite valve. Fold rather high but not well distinguished from flanks; beginning slightly further back than sulcus and bearing two strong, wide, angulate or rounded ribs, which leave an intermediate groove of approximately equal width. Flanks smooth or bearing one rib on each. Ventral interior with rather large spondylium, sessile in posterior extreme and anteriorly elevated on median septum extending forward of it (see Pl. 30, figs. 23–26); spondylium occupying about one-third of valve length, with muscle tracks apparent on it. Both sides of median septum of gerontic specimens bearing thick ridges, becoming rather high, supporting sides of spondylium and continuing anteriorly to septum. Teeth small. Dorsal interior with rather long and narrow camarophorial trough on median septum, which increases in height forward to become very high and after that fades sharply (see Pl. 30, figs. 23, 24, 26); walls of camarophorium joining underside of hinge plate, camarophorium continuing free in anteroventral direction and extending further forward than spondylium of opposite valve. Hinge plate short, concave, except in its apex, where it bears a big

cardinal process of trigonal section and with lamellar myophore. Sockets long, narrow, located between lateral extreme of hinge plate and very narrow and low ridge separating them from valve wall. Crura initially following direction of camarophorium and later directing more ventrally. Intercamarophorial plate seen only in one specimen and reduced to very low and narrow elevation, located on posterior part of floor of camarophorium.

Discussion. The species is assigned to *Cyrolexis* because of its internal characteristics, although externally it resembles more closely some species of *Coledium* Grant, 1965. *Cyrolexis granti* is distinguished from *C. haquei* and other species of *Cyrolexis* by its transverse form, less numerous ribs on fold and sulcus, normally smooth flanks, and fold that is little differentiated from them. Exteriorly it looks like *Coledium explanatum* (McChesney, 1860) and particularly *C. globulinum* (Phillips, 1834) of Grant (1965a). It is distinguished from the former by the absence of the intercamarophorial plate, smaller size, more transverse form, and weaker ribs. In *C. globulinum* the presence of the intercamarophorial plate has not been firmly established; Grant (1965a, p. 120) says: 'intercamarophorial plate not observed, probably present', and Tschernyschew (1902) does not refer to it. If such a plate does not exist, *C. globulinum* could belong to *Cyrolexis* and it would be close to *C. granti*. Both differ externally by the more transverse form and even smaller size of the Cantabrian species. *C. granti* is now the oldest species attributed to the genus, which was considered restricted to the Permian.

Family STENOSCISMATIDAE Oehlert, 1887
Subfamily STENOSCISMATINAE Oehlert, 1887
Genus STENOSCISMA Conrad, 1839

1965a *Stenosisma* Conrad; Grant, p. 138.

Type species. Terebratula schlotheimi von Buch, 1835.

Stenosisma winkleri sp. nov.

Plate 29, figs. 13, 14; Plate 30, figs. 1-22; text-figs. 6, 7

Derivation of name. Dedicated to Dr. C. F. Winkler Prins.

EXPLANATION OF PLATE 30

Figs. 1-22. *Stenosisma winkleri* sp. nov. 1-5, $\times 2$. Holotype, DPO 7005, dorsal, ventral, lateral, anterior, and posterior views showing the remains of the stolidium. 6-9, $\times 2$. Paratype, DPO 7007, dorsal, ventral, anterior, and posterior views. 10-13, $\times 2$. Paratype, DPO 7008, dorsal, ventral, anterior, and posterior views. 14-17, $\times 2$. Paratype, DPO 7009, dorsal, ventral, anterior, and posterior views. 18-21, $\times 2$. Paratype, DPO 7010, dorsal, ventral, anterior, and posterior views. 22, $\times 4$. Paratype, DPO 7206, fragmentary specimen showing skeletal internal structures of the cardinal region; dorsal valve above.

Figs. 23-26. *Cyrolexis granti* sp. nov. 23, 24, $\times 5$. Paratype, DPO 7286, internal mould of both valves and latex cast of posterior region showing spondylium and teeth in ventral valve and hinge plate and camarophorium without intercamarophorial plate in dorsal valve. 25, $\times 5$. Paratype, DPO 7284, posterior view of an internal mould of both valves showing spondylium and camarophorium. 26, $\times 9$. Inclined view of the same specimen to show mould of the cardinal process.



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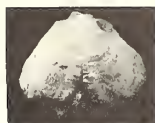
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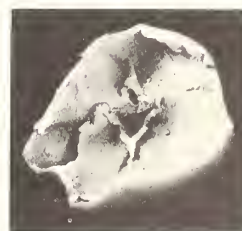
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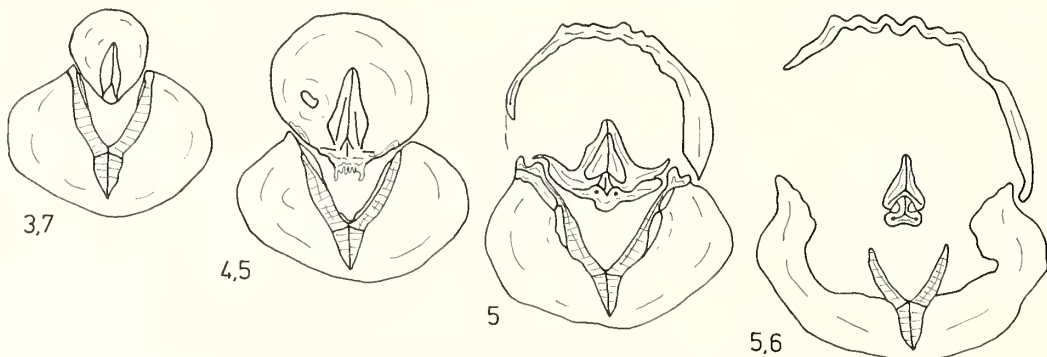


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Material. Holotype (DPO 7005, Pl. 30, figs. 1-5), 75 paratypes (DPO 7006-7076, 7142-7145) and 135 other specimens (DPO 7077-7141, 7146-7205) from the type locality; 5 paratypes (DPO 7206-7210) and 42 other specimens (DPO 7211-7252) from a locality NE. of Pinos (province of León = locality 29 of Winkler Prins, 1968), and 30 specimens (DPO 7253-7282) from other occurrences.

Type locality. Marly limestone of the Escalada Formation, at about 30 m above its base, of upper Kashirian age (according to van Ginkel, 1965), from a small cove on the coast north-east of Hontoria (province of Oviedo). Longitude $1^{\circ} 41' 43''$, latitude $43^{\circ} 27' 8''$.

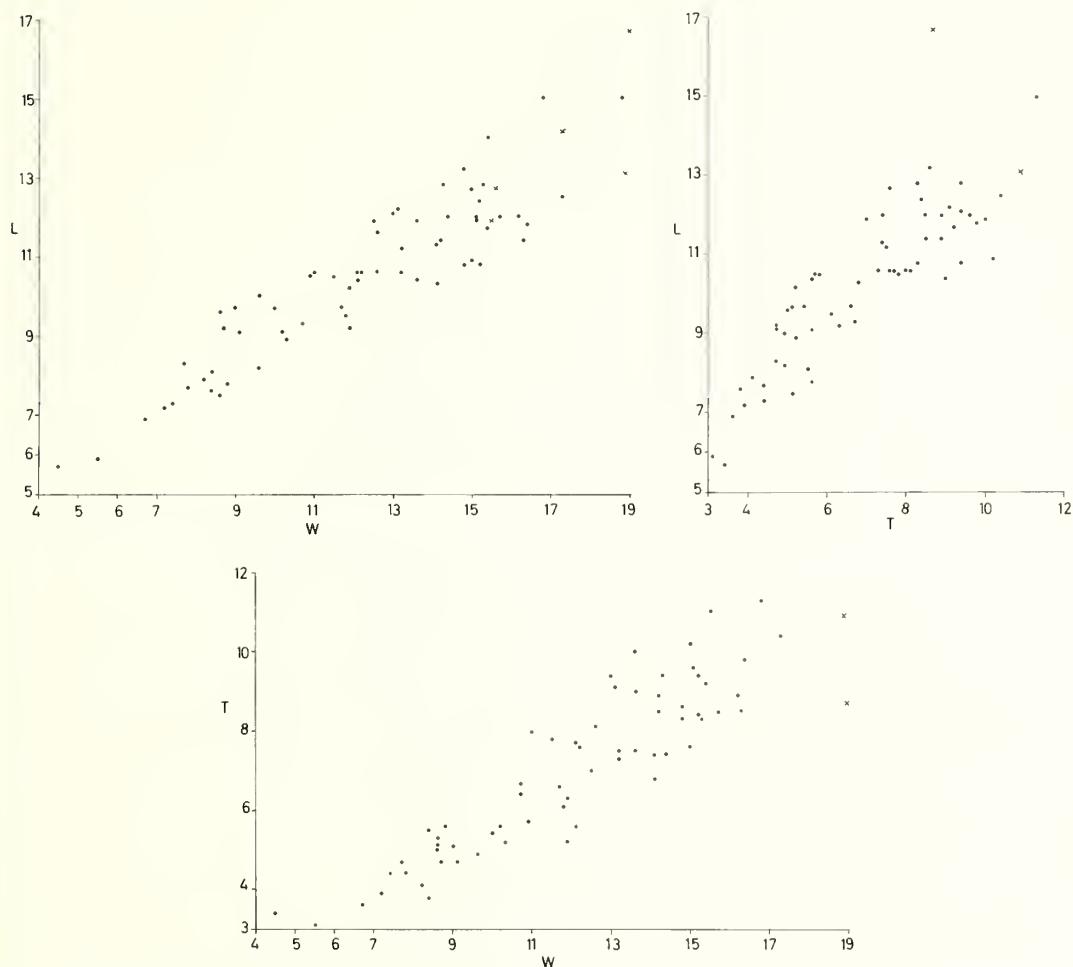
Diagnosis. *Stenosisma* with trigonal outline, very expanded anteriorly, transverse. Fold normally with four to five strong ribs and sulcus with one fewer. Flanks smooth or with one, or exceptionally two, ribs on each. Ribs beginning rather far anteriorly to beak. Short stolidium, little developed and inappreciable for most of the specimens.



TEXT-FIG. 6. *Stenosisma winkleri* sp. nov. Transverse sections of specimen DPO 7207 showing internal shell structures. Distances from the ventral beak in mm, $\times 4$.

Description. Small to medium-sized shell, outline trigonal, widely spreading near anterior margin, transverse although juvenile specimens slightly elongated, dorsibiconvex; anterior commissure uniplicate. Stolidium in some specimens (see Pl. 30, figs. 1-5) extending to anterolateral and, sometimes, anterior margins of both valves, but always only very narrow, reaching a few millimetres in width. Ventral valve gently convex, beak pointed, and strongly incurved dorsally. Small and triangular delthyrium, constricted by narrow and disjunct deltidial plates, leaving triangular foramen. Sulcus beginning from one-third to one-half of valve length, shallow and flat-bottomed but widening to one-third of valve width anteriorly where it deepens as it curves dorsally into the tongue; sulcus is bounded at both sides by wider and more rounded rib than those of its floor. Posterolateral flanges strongly developed, high, and overlapped by those of opposite valve. Dorsal valve more strongly convex. Beak pointed, ventrally directed into ventral valve. Fold beginning at about mid-length, low except anteriorly where the flanks fall away steeply, top flat or gently arched. Median ribs wider than interspaces, slightly diverging forward, angular in most specimens; lateral ribs developed later in life, sometimes by bifurcation. Number of ribs variable (see Pl. 30, figs. 4, 8, 12, 16, 20), most frequently 4-5 on fold (some specimens bearing 3 or 6, very few 2, and only one with 8); sulcus one less than fold; flanks usually smooth or with one or, more rarely, 2 ribs each, generally

beginning further anteriorly; weaker than those on sulcus and fold. Growth lines usually weak, but occasionally stronger. Dimensions of the holotype in mm: $L = 12.7$; $W = 15$; $T = 7.6$. It bears 5 ribs on the fold. The dimensions of other specimens are in text-fig. 7.



TEXT-FIG. 7. Dimensions of *Stenoscisma winkleri* sp. nov. in mm. • specimens from the type locality; x specimens from locality 29 of Winkler Prins (1968), and from other localities nearby.

Ventral interior with wide spondylium supported by very low median septum duplex (see text-fig. 6 and Pl. 30, fig. 22), posterior part buried by secondary shell, so spondylium appears apically sessile; septum seen anteriorly with a height just over 1 mm, extending slightly anterior to spondylium; length of spondylium about one-third of valve length. Umbonal chambers can be full of secondary shell. Teeth strong, short, upper part rounded and each one having a lateral exterior crenulation. Dorsal interior with low and narrow camarophorial trough, anteroventrally directed and extending slightly in front of spondylium; supported by thin median septum

duplex, with height increasing towards anterior edge of trough, becoming very high, and from there decreasing parabolically, disappearing 1 or 2 mm anteriorly. Intercamarophorial plate duplex, high and long, occupying all the length of trough, posterior part supporting hinge plate. Posterior part of camarophorium can be buried by secondary shell and intercamarophorial plate not discernible to its anterior edge, in front of hinge plate. Hinge plate undivided, supporting on its apex a big and wide cardinal process, with myophore of high and thin lamellae; inner hinge plates extending rather more anteriorly than outer ones. Crura curving in ventral direction. Sockets narrow, short, and located at anterolateral extremities of outer hinge plates.

Discussion. *S. winkleri* is about the same size as *S. schlottheimi*, but it differs from the latter by its more trigonal outline with the maximum width nearly at the front, lower fold, generally stronger and more numerous ribs on fold and sulcus, and smaller developed stolidium. It also resembles *S. crumenum* (Martin, 1809) and *S. mutabile* (Tschernyschew, 1902), but is smaller, less thick, and its stolidium is less well developed than in both of these species; in addition *S. crumenum* has more strongly ribbed flanks and *S. mutabile* in adulthood is more fully ribbed than *S. winkleri*. The species is known from San Emiliano, Beleño, and Escalada Formations, which are upper Bashkirian to upper Kashirian age.

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TWO CARBONIFEROUS BLASTOIDS FROM SCOTLAND

by D. B. MACURDA, JUN.

ABSTRACT. The two fissiculate blastoids, *Astrocrinus tetragonus* (Austin and Austin, 1843) and *Hadroblastus(?) benniei* (Etheridge and Carpenter, 1886), occur together in Early Carboniferous Viséan (D) sediments of Scotland. *Astrocrinus* is a small, free-living eleutherozoic blastoid characterized by well-developed surface ornament. The nodes are interpreted as spine bases which, together with some brachioles, probably stabilized the animal on its substrate in periods of higher energy. *H. (?) benniei*, a stemmed blastoid formerly identified as *Phaenoschisma? benniei*, extends the known geographic range of *Hadroblastus* from North America to the British Isles, and the stratigraphic range into the Upper Viséan, if the species assignment is correct.

IN their definitive study of the blastoids in 1886, Etheridge and Carpenter listed three Lower Carboniferous blastoids from Scotland. The fragmentary nature of many of these has made their interpretation difficult. *Astrocrinus tetragonus* (Austin and Austin, 1843) is one of the very few free-living (eleutherozoic) blastoids; it is also found in England and Ireland. A second species, which is known only from Scotland, was originally described as *Phaenoschisma benniei* Etheridge and Carpenter, 1886. The third species was represented only by isolated ambulacra and thought to be a spiraculate blastoid (Etheridge and Carpenter 1886, p. 279; pl. II, figs. 38-42). Breimer and Macurda (1972) reviewed the first two species in a study of the phylogeny of the fissiculate blastoids. Because of its unique morphology, Austin and Austin (1843) erected the family Astrocrinidae for *Astrocrinus*, and it remains the only genus in this family. Breimer and Macurda (1972) described the internal structure of *A. tetragonus* and briefly discussed its growth and geographic occurrence. Etheridge and Carpenter (1886) discussed the nodes on the plates of *A. tetragonus* and concluded that they were perforate and probably bore a spine which articulated on them. Study of these nodes by scanning electron microscopy has shown them to be imperforate and of importance in deducing the life mode of the animal. Further preparation of specimens of *P. benniei* has shown that this species almost certainly belongs to the North American Mississippian genus *Hadroblastus* and thus extends its geographic range.

DIAGENESIS, BIOSTRATINOMY, AND PALAEOECOLOGY

The Scottish blastoids discussed herein have been collected from a sequence of Viséan D Zone limestones and calcareous shales. Etheridge and Carpenter (1886) listed their specimens as coming from the shales above No. 1 and No. 2 Limestones of the Lower Carboniferous Limestone group near Midlothian and Fife (*Astrocrinus*) and the Shale above the No. 2 Limestone in the East Salton and Kidlaw Quarries near Gifford, Haddingtonshire (*Hadroblastus(?) benniei*). Subsequent collections were made during the first part of the twentieth century by James Wright,

[Palaeontology, Vol. 20, Part 1, 1977, pp. 225-236, pls. 31-32.]

whose collection is now in the Royal Scottish Museum. His material bears the locality labels 'Carlops, Peeblesshire' and 'No. 1 Bed, Invertiel, Fife'. These materials were apparently obtained as a by-product of Wright's study of *Allagecrinus* from the localities in the Lower Limestone Group (Wright 1941). George (1971) reviewed the stratigraphic complexities and biostratigraphy of the Lower Limestone Group. The Viséan–Namurian boundary occurs somewhere near the top.

The blastoids from the Lower Limestone Group are almost invariably crushed. This is not unexpected, as they are preserved in shales which underwent compaction. The thecae of *Astrocrinus* are compressed vertically and adjacent plates are strongly displaced. One frequent zone of failure is through the base of a theca along a line connecting the C and E ambulacra. This particularly obscures the relationships of the basal plates. *H.(?) benniei* is crushed flat and usually only partial thecae are recovered. Preservation in the shale, however, has had one beneficial effect. The skeletal microstructure (stereom) of echinoderms is an open lattice with numerous pores. Diagenetic calcite cements crystallize in optical continuity with the stereom and overgrow it externally. This most always obliterates surface detail, and the internal fabric is often disrupted. Preservation in fine-grained sediments instead of skeletal limestones may reduce the severity of the cementation process, resulting in excellent external and internal preservation of the blastoid stereom (e.g. Macurda 1973). The stereom is clearly evident within the plates of the specimen of *H.(?) benniei* in Plate 32, figs. 5, 8, when it is immersed in xylene. It is also evident on the surface of the plates of some specimens of *A. tetragonus* (Pl. 31, figs. 3, 6). The preservation of the surface detail on the plates of these blastoids is very good; this would suggest they are essentially preserved in the environment in which they lived. After death, they remained unburied long enough for the tissue binding the brachioles, ambulacral covering plates, and the stem in *H.(?) benniei*, to decompose, permitting disarticulation.

H.(?) benniei is a blastoid that is conventional in appearance and had a stem cicatrix. There is no morphologic evidence to indicate an unusual mode of life; it was probably a current-seeking (rheophilic) blastoid (Type I of Breimer and Macurda 1972). *A. benniei* is highly unusual. It is as though the lower half of the blastoid were stunted and grew to the side. It has a quadrate outline (Pl. 32, figs. 4, 7, 9), has no stem cicatrix, lacks any attachment scars, and thus was free living. The theca is always small (less than 10 mm) and even moderate oceanic swells or waves or tidal currents would exert a lifting force which would continually reorientate the animal, perhaps detrimentally. Thus it would appear to have lived in quiet or deep-water environments or might have had some special adaptations permitting it to cope with periods of higher environmental energy. The stratigraphic relationships of the Lower Limestone Group are not indicative of deeper water; the geographic extent of *Astrocrinus* and its local abundance suggest it was a functionally successful design. The ornament found on the surface of the plates is probably important in understanding the life mode of *Astrocrinus*. Most blastoid plates were secreted by deposition of calcite laterally along the edges of the plates, and growth lines are evident on the external surface. In *Astrocrinus* these are only occasionally evident on the sloping walls of the ambulacral sinus formed by part of the deltoid body and RD sector of the radial. Nodes occur on the upper part of the deltoid body along the

crest and its sloping sides (Pl. 31, figs. 1, 3). They can have a row-by-row arrangement parallel to the radiodeltoid suture, suggesting formation as the plate grew aborally. Since their growth was upward, they represent deposition on the external surface, either contemporaneously with the growth-line formation or just subsequent to it. Those adjacent to sutures are of equal magnitude to those formed earlier and there is no gap as one approaches the radiodeltoid suture. The maximum diameter of the nodes is 0.15 mm and their height is about the same. There are approximately twelve radially disposed grooves on the side of each node; these terminate below the tip of each node. Nodes are also present on the upper half of the regular radials (above the aboral tip of the ambulacrum, external to the ambulacral sinus). Ornament on the lower half of the radials assumes a more linear appearance, the nodes assuming a laterally directed ridge-like aspect (Pl. 32, fig. 3). On the attenuated D radial and the bordering limbs of the C and E radials, ornament consists of sharp, linear ridges (Pl. 32, figs. 1, 2). These are nearly perpendicular to their respective sutures.

Articular surfaces between larger plates in echinoderms are usually characterized by non-porous stereom, as are the fulcral ridges of articulations in crinoids (Macurda and Meyer 1975) or the mammelons of echinoids (Jensen 1972). The surfaces on which small spines articulate in echinoderms are less obviously expressed in the stereom. Comparative study of the morphology of these surfaces should be helpful in determining the presence of spines in fossil echinoderms. The arms of the ophiuroid *Astrophyton* bear prominent spines used to snare prey, but the surface expression of the articulation of the spine with the arm is not well defined (Macurda 1976). The Devonian crinoid *Arthroacantha* bears spines on the surfaces of the basals and radials (e.g. Kesling and Chilman 1975, pl. 29, figs. 1-3). These spines may be at least 5.0 mm long and the diameter of the raised area where they articulate is only 0.3 mm. Without preserved spines, the raised areas would probably be merely interpreted as 'surface ornament'. It is tempting to suggest that each node of *Astrocrinus tetragonus* bore some type of spine and that the grooves on the side of each node represent points of insertion for muscles or ligaments to articulate the spine (Pl. 31, fig. 7). Etheridge (1876) reported and illustrated a microscopic spine adhering to one of his specimens by some particles of matrix, but it was not attached in place. No spines were observed during this study. The stereom of each node is apparently solid. Initially there are approximately six grooves (Pl. 31, fig. 2) but, as the node becomes larger, new grooves are inserted in intervening spaces. The tip of a node is a blunt, low hemispherical cap (Pl. 31, fig. 4). There is no differentiation of the stereom around the base of a node.

In the absence of the direct preservation of articulated spines, their presence in *Astrocrinus* remains speculative, but the morphology of the nodes is suggestive of their presence. The following discussion attempts to interpret the palaeoecology of *Astrocrinus* assuming their presence. The purpose of the spines was protective and they projected into the surrounding water. The animal sat on the substrate with the area beneath the D ambulacrum in contact with the substrate (see Pl. 32, figs. 4, 7, 9). The brachioles from the D sides of the C and E and the attenuated D ambulacra were splayed on to the substrate to help stabilize the organism in this position; the AB interarea projected uppermost. The linear ornament below the D ambulacrum also served to resist displacement due to waves or currents. (The D sides of the C

and E ambulacra are wider than their opposite sides and less steep; this would have allowed the brachioles to project more nearly parallel to the substrate.) Spines borne in the EA, AB, and BC interareas on the body of the radials immediately below these interareas projected outward to form a protective forest of spines; some of those on the radial bodies may also have projected into the substrate. Thus, in spite of its small size, *Astrocrinus* could stabilize and position itself on the substrate through a combination of linear ornament, spines, and brachioles. The brachioles of the A and B ambulacra functioned normally but those of the D and parts of C and E were utilized to provide fixity for this free-living blastoid.

SYSTEMATIC PALAEONTOLOGY

Class BLASTOIDEA Say, 1825

Order FISSICULATA Jaekel, 1918

Family ASTROCRINIDAE Austin and Austin, 1843

Genus ASTROCRINUS Morris, 1843

1843 *Astracrinites* Austin and Austin, p. 110.

1843 *Astrocrinus* Morris, p. 49.

1848 *Zygocrinus* Bronn, p. 1381.

Type species. *Astracrinites tetragonus* Austin and Austin, 1843.

Astrocrinus tetragonus (Austin and Austin)

Plate 31, figs. 1-7; Plate 32, figs. 1-4, 7, 9; text-fig. 1

1843 *Astracrinites tetragonus* Austin and Austin, p. 110.

1843 *Astrocrinus tetragonus* Morris, p. 49.

1876 *Astracrinites benniei* Etheridge, p. 103.

Scottish material. Royal Scottish Museum specimen numbers 1958.1.2355, 2360-2364, 2367, 2376, 2378-2380.

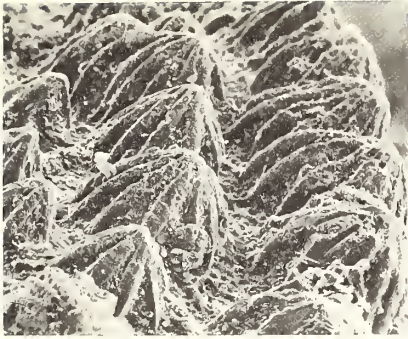
Description. Theca squat, ovoid in lateral view, pentagonal, asymmetric in oral view. Stem cicatrix lacking, animal being eleutherozoic with development of bilateral symmetry along plane of AB interarea and D ambulacrum (Pl. 32, figs. 4, 7, 9). AB, BC, and EA interareas protuberant, while CD and DE form a continuous, slightly convex arc in oral view due to shortened D ambulacrum. A and B ambulacra

EXPLANATION OF PLATE 31

Astrocrinus tetragonus (Austin and Austin, 1843); Lower Limestone Group, Lower Carboniferous; Carlups, Peeblesshire, Scotland. Scanning electron micrographs.

Figs. 1-7. 1, inclined view of nodes on deltoid, $\times 115$; R.S.M. 1958.1.2363. 2, incipient node on deltoid, $\times 455$; R.S.M. 1958.1.2363. 3, plan view of deltoid, oral direction at top, $\times 35$; R.S.M. 1958.1.2380. 4, fully developed node on deltoid, $\times 350$; R.S.M. 1958.1.2363. 5, brachiolar facets on edge of ambulacrum, oral direction to left, $\times 115$; R.S.M. 1958.1.2363. 6, detail of stereom on wall of ambulacral sinus, $\times 685$; R.S.M. 1958.1.2380. 7, fully developed node on deltoid with top broken off, $\times 455$; R.S.M. 1958.1.2363.

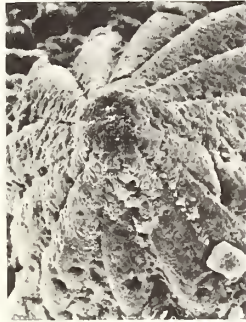
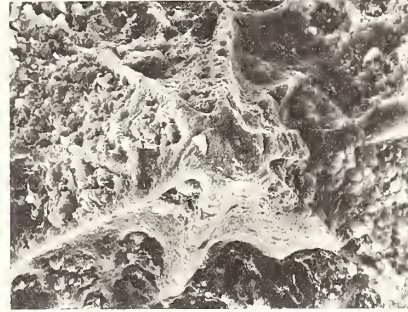
(R.S.M., Royal Scottish Museum.)



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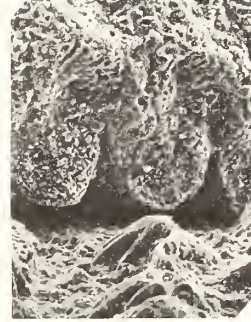


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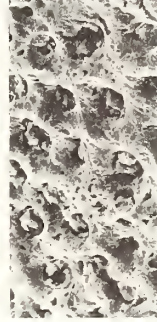


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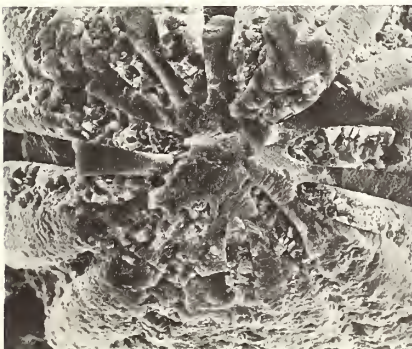
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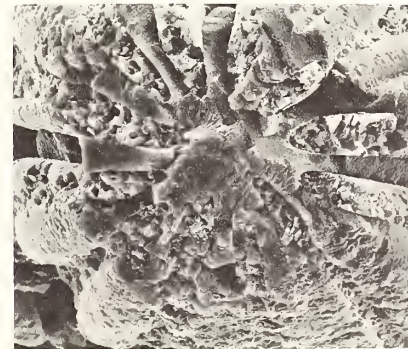
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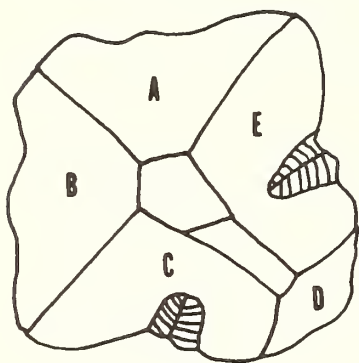
7



MACURDA, blastoids from Scotland

convex, set within broad shallow ambulacral sinus and extending to near base of theca; C and E ambulacra slightly longer, extending to base of outline in lateral view and visible in aboral view, recurving inward. D ambulacrum short, flat, confined to upper surface of theca. Length 2.32 mm; width, A-CD, 3.65 mm; AB-D, 4.48 mm.

Basalia two, extending from centre of aboral surface half-way up lateral surface beneath D ambulacrum (text-fig. 1). Outline elongate, narrow, pentagonal. No stem



TEXT-FIG. 1. *Astrocrinus tetragonus*, aboral view, Royal Scottish Museum specimen number 1958.1.2376, $\times 12$. Compare with Plate 32, fig. 7. Radials A-E labelled. Drawn with camera lucida.

cicatrix. Basal on aboral surface flat, has two equal short edges against narrow bases of A and B radials (0.56 mm each); basal extending toward and narrowing slightly toward D ray. Edge against C radial of about equal length to A and B (0.48 mm), E about twice as long (0.88 mm); interbasal suture extends diagonally from a point near a centre line of E ambulacrum diagonally towards B side of C radial. Interbasal suture very slightly sinuous. Other basal convex in lateral view, quadrate in plan view, elongate (1.20 mm), with long edges against C and E radials and narrow edge against D radial half-way up lateral edge of theca; maximum width 0.40 mm. Lower basal ornamented with pustulose ornament, upper basal with a few irregular ridges parallel to long axis of plate (Pl. 32, fig. 1).

EXPLANATION OF PLATE 32

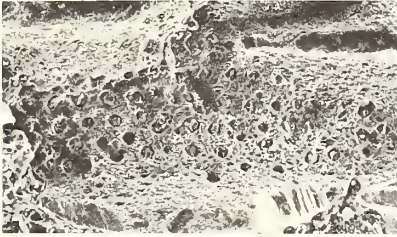
Figs. 1-4, 7, 9. *Astrocrinus tetragonus* (Austin and Austin, 1843). 1-3, Lower Limestone Group, Lower Carboniferous; Carlops, Peeblesshire, Scotland. 4, D₁ beds, Viséan, Lower Carboniferous; foreshore Oyster Bay, Fenit, Co. Kerry, Ireland. 7, 9, Lower Limestone Group, Lower Carboniferous, Invertiel, Fife, Scotland. 1, D deltoid (right side) and bordering C and E radials and basal (left centre), $\times 30$; R.S.M. 1958.1.2361. 2, detail of ornament of D deltoid of fig. 1, $\times 285$. 3, radial bodies, A right, B left, $\times 50$; R.S.M. 1958.1.2363. 1-3, scanning electron micrographs. 4, oral view of specimen preserved on limestone surface, A ambulacrum at 9 o'clock, $\times 6$; N.M.I. G.40.1965. 7, 9, aboral and oral views with A and B ambulacra at 12 o'clock respectively, $\times 7.5$; R.S.M. 1958.1.2376. Specimens in 4, 7, and 9 coated with sublimate of ammonium chloride.

Figs. 5, 6, 8. *Hadroblastus(?) benniei* (Etheridge and Carpenter, 1886); Lower Limestone Group, Lower Carboniferous; Carlops, Peeblesshire, Scotland. 5, 8, inclined oral (centred on anal interarea) and lateral views of crushed specimen in xylene, $\times 4.8$; R.S.M. 1958.1.2461. 6, left side of specimen in fig. 5 coated with sublimate of ammonium chloride, $\times 7.5$.

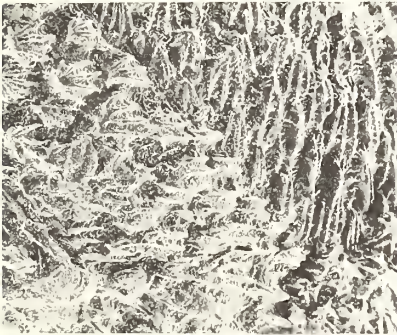
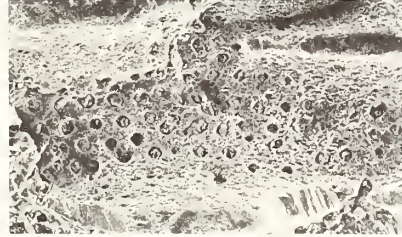
(R.S.M., Royal Scottish Museum; N.M.I., National Museum of Ireland.)



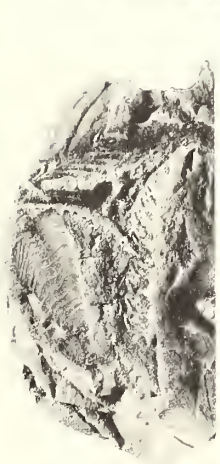
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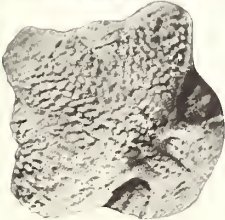
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7



8



5



9

MACURDA, blastoids from Scotland

Radials five, A and B of similar shape; D limbs of C and E truncated, and D reduced in size due to bilateral symmetry. A and B radials pentagonal in plan view with narrow base (0.52 mm), lateral sides diverge rapidly outward to maximum width at aboral tip of deltoids (2.92 mm), upper edges extend into ambulacral sinus at a right angle to axis of sinus. Radials A and B triangular in lateral view, being slightly convex from origin of radial outward in both an aboral and oral direction; lower edge slightly concave. RB sector narrow, straight both parallel and perpendicular to RB axis; RB growth front straight (RB 1.64 mm; RBF 0.26 mm). RB sector merges smoothly with RR sector. Latter is very slightly convex parallel to and strongly convex perpendicular to RR axis; RR growth front straight (RR 1.20 mm; RRF 2.84 mm). RB and RR sectors ornamented with nodose ornament or discontinuous linear ridges. No growth lines visible. RD sector at sharp angle to RR sector, forming part of ambulacral sinus, slightly convex parallel to and straight perpendicular to RD axis. RD growth front very slightly convex (RD 1.60 mm; RDF 1.28 mm). Outer part of ambulacral sinus ornamented with nodose ornament; inner part smooth. AB interarea slightly larger than AE or BC. C and E radials similar except RB sectors much shorter with much longer radial-basal suture, and D side of each is about one-half the size of the other half due to the truncate D ambulacrum. No ambulacral sinuses along D sides of C and E radials. D limb of E radial in contact with DE deltoid along narrow suture bordering ambulacrum; D limb of C radial in contact with hypodeltoid. D radial small, relatively flat. RB sectors (RB 1.44 mm; RBF 0.04 mm) and lower half of RR sectors similar in size to those of A and E radials but upper part of RR sectors and RD sectors much shortened and reduced, bordering reduced D ambulacrum (RR 1.08 mm; RRF 1.36 mm; RD 0.72 mm; RDF 0.60 mm). D radial beneath ambulacrum and bordering limbs of C and E radials; discontinuous linear ridges perpendicular to radial and radial-basal sutures (Pl. 32, figs. 1, 2).

Deltoids four; three of equal size, DE reduced. Regular deltoid rhombic in plan view, convex in lateral view. Deltoid lip small, hexagonal with edge bordering oral opening and interdeltoid sutures bearing ambulacral tract, sloping downward towards plate edges. Deltoid lip constricts aborally along deltoid-ambulacral suture to adoral end of hydrospire clefts. Central portion of deltoid lip flat, being higher than ambulacral tracts and hydrospire clefts. Deltoid body rhombic in outline, expanding aborally from narrow constriction of deltoid at adoral ends of hydrospire clefts. Body bordered laterally by hydrospire clefts and aborally by radiodeltoid sutures; all of these edges straight (Body L. 1.80 mm). Plane of radiodeltoid sutures nearly horizontal. Deltoid body convex lengthwise, with greatest height being in median position along a rounded crest. Axis of crest may be ornamented by nodes along centre of crest (Pl. 31, fig. 1) or these may merge to be a semicontinuous ridge. Sides of deltoid body slope steeply downward into ambulacral sinus, ornamented by nodes which may form a row paralleling the crest. Broad growth lines may be visible parallel to radiodeltoid suture. Body smooth near ambulacra. As on radial, a node has a blunt top but the base is fluted by parallel grooves. (Del. L. 2.40 mm; Gr. Ad. W. 0.56 mm; Min. W. 0.40 mm; Gr. Ab. W. 1.28 mm; DR 1.40 mm.)

DE deltoid smaller, asymmetrical. Deltoid lip as for other deltoids, body much reduced because of asymmetry. Form of DE deltoid body similar to that of regular

body but about one-third its size; radiodeltoid suture with D radial long whereas that with E radial short. Furthest aboral extension of deltoid thus near to ambulacrum (Body L. 0.64 mm; Gr. Ab. W. 0.52 mm).

Anal deltoids four: a superdeltoid bordering oral opening, two cryptodeltoids (internal) and a hypodeltoid. Size of superdeltoid similar to deltoid lip of regular deltoid. C cryptodeltoid large, D cryptodeltoid small. Hypodeltoid a relatively large plate, pentagonal, with concave adoral edge bordering anus, two straight lateral edges bordering C and D ambulacra, and slightly convex radial-hypodeltoid sutures; D side of plate larger. Plate relatively flat, slopes downward from D to C ambulacrum. Some nodal ornament (HD L. 0.48 mm; W. 0.88 mm).

Ambulacra five; D much shortened and reduced. Normal ambulacra linear in plan view, convex in lateral view. A and B ambulacra (L. 2.0 mm) curve through 90° while C and E ambulacra (L. 2.4 mm) curve through 120° and are visible in aboral view. Aboral tips of C and E ambulacra more closely approach each other (1.40 mm) than do aboral tips of A and B ambulacra (2.20 mm; Pl. 32, fig. 7). A and B ambulacra in ambulacral sinus. B side of C ambulacrum and A side of E ambulacrum also have sloping wall of sinus but D sides flush with bordering radials. Ambulacra convex in cross-section (W. 0.68 mm) with median depression along ambulacral tract. Lancet exposed along median adoral two-thirds of ambulacrum. Brachiolar facets along lateral sloping sides of ambulacrum (Pl. 31, fig. 5). Side plates seven per mm, quadrate, with slightly convex admedial edge and straight aboral edge. Adoral admedial edge of plate embayed by triangular outer side plate. Edge of side plate against next adoral side plate straight as is adoral suture against outer side plate. Laterally side plate tapers to a point or narrow rounded tip. Outer side plates widest along lateral edge of ambulacrum. Brachiolar facet ovoid, formed equally from side plate (aboral half) and outer side plate (adoral half) (L. 0.14 mm; W. 0.12 mm).

D ambulacrum short (L. 1.2 mm), lanceolate in plan view (W. 0.48 mm), flat in lateral view, convex in cross-section. Less than half of lancet exposed in adoral half of ambulacrum.

Ambulacra separated from adjacent radials and deltoids by hydrospire clefts which extend full length of the ambulacrum and provide entrance to the ten hydrospire groups. Two hydrospires per group except in those of anal interarea and E side of D ambulacrum, where there is only one.

Oral opening pentagonal, bordered by four deltoids and superdeltoid (W. 0.28 mm). Adoral edges of plates bearing minor grooves of ambulacral tract.

Remarks. The description of the external morphology is derived from R.S.M. 1958.1.2376 (Pl. 32, figs. 7, 9), and measurements cited above pertain to this specimen. A previous repository and locality citation for this specimen (Breimer and Macurda 1972, pl. XI, figs. 4, 7) was incorrect. Details of the super- and cryptodeltoids and hydrospires are summarized from Breimer and Macurda 1972.

Abbreviations for plate descriptions and measurements are given in Breimer and Macurda 1972. Micrographs were taken with a Japan Electron Optic-Laboratory Model JSM-U3 scanning electron microscope. Specimens were coated with 500 angstroms of gold and photographed with Polaroid PN type 55 film at 15 KV.

Family NEOSCHISMATIDAE Wanner, 1940

Genus HADROBLASTUS Fay, 1962

Type species. *H. convexus* Fay, 1962.

Hadroblastus(?) *benniei* (Etheridge and Carpenter)

Plate 32, figs. 5, 6, 8

1886 *Phaenoschisma benniei* Etheridge and Carpenter, p. 278, pl. II, fig. 37; pl. IV, figs. 5, 6.

1972 ?*Phaenoschisma benniei* Breimer and Macurda, p. 18, pl. V, figs. 8, 11, 13.

Scottish material. British Museum (Natural History) specimen numbers E666, E1114, E1115; Royal Scottish Museum specimen number 1958.1.2461.

Description. Theca small, biconical, vault and pelvis subequal. Pelvis conical, broad; vault low, with break in profile at junction of radial and deltoids. Cross-section pentagonal (at angular tip of ambulacra); greatest width median at aboral tip of ambulacra. Height and width subequal, near 10 mm or less.

Basals one-half of conical pelvis, pentagonal in plan view, very slightly concave in lateral profile. Stem cicatrix small, at very base of theca. Azygous basal not preserved. Zygous basal pentagonal in plan view with straight edges. Median and lateral BR sectors very slightly concave parallel to BR axis; median convex, lateral straight normal to BR axis. Adjacent sectors merge smoothly. Growth lines strong. Typical ZBL 1.8 mm; ZBW 2.0 mm; ZBOpt 2.1 mm; ZBBR 1.7 mm; ZBBRF 1.0 mm.

Radial pentagonal in plan view. Lower edge radial convex, lateral edges slightly convex, top straight, slightly concave inward. In plan view ambulacral sinus occupies one-half of upper part of radial. In lateral profile radial V-shaped with upper two edges subequal, straight profile, lower edge concave. RB sector straight or very slightly convex parallel to RB axis, slightly concave normal to it, merges smoothly with RR sector. Latter straight parallel to RR axis and convex normal to it. RD sector grew mostly within an ambulacral sinus, straight parallel and normal to RD axis. Narrow external RD growth sector borders ambulacral sinus. Striated ornament (growth lines) paralleling sutures in RB, RR, and external part of RD sectors; small double U-shaped lip at aboral end of ambulacrum at origin of radial. Hydrospires occupy full width RD sector until eight or nine hydrospires formed.

Deltoid hexagonal in plan view with straight DD, concave DAF, and straight DRF. Deltoid slightly convex to very slightly concave in lateral profile, with crest forming dominant part of plate. Adoral edge of plate (deltoid lip) prominent, with adorally directed V-shaped rim bordering ambulacral tract. Deltoid crest originates just behind small depression paralleling adoral rim. Crest sharp, directed downward from oral opening. Sides of crest slope moderately downward, with hydrospire slits across DRF until eight to nine hydrospires formed. Formation of hydrospires then ceases and deltoid crest bifurcates in median part of deltoid body to form two aborally diverging ridges which border ambulacral sinus. Median aboral part of deltoid body rhombic, concave in cross-section.

Number of anal deltoids unknown. Relatively large hypodeltoid with external growth sector present. Hypodeltoid pentagonal, with straight lateral borders and

convex hyporadial sutures, each with an aborally directed angular bend in the middle.

Ambulacra five, sublanceolate in plan view, slightly convex in lateral view extending half-way down theca. Ambulacrum convex in cross-section, with median depression along ambulacral tract. Lancet narrowly exposed, apparently over most of the ambulacral length. Three side plates per mm. Aboral lateral edge of each side plate embayed by a large triangular outer side plate. Side plate pentagonal with straight adoral edge which intersects median line of ambulacrum at an angle; convex admedial edge; straight aboral medial edge which parallels adoral edge; straight aboral lateral edge against outer side plate, and narrow, slightly convex lateral edge which forms part of outer edge of ambulacrum. Large elliptical brachiolar facet on outer sloping side of ambulacrum (Pl. 32, fig. 6), formed equally on side plate (aboral half) and outer side plate (adoral half). Arcuate trough borders aboral margin of brachiolar facet. Four or five minor grooves per side plate border main ambulacral groove; present also on adoral margin of ambulacral side grooves.

Ten(?) hydrosipre groups. Maximum of eight to nine in regular groups, bordering ambulacrum in shallow ambulacral sinus. Some visible on C side of anal interarea, presumed to be present on D side as well (R.S.M. 1958.1.2461). Number apparently reduced in anal interarea.

Stereomic microstructure is well preserved in some specimens.

Remarks. The above description is a composite taken from specimens in the Royal Scottish Museum and the British Museum (Natural History). The specimens are crushed and fragmentary, precluding accurate measurement, and only a few have been recovered.

Etheridge and Carpenter (1886) originally described this species as *Phaenoschisma benniei*. Breimer and Macurda (1972) listed this assignment with a question mark. Restudy and further preparation of the material from the Royal Scottish Museum revealed agreement on almost all determinable characters with the definition for *Hadroblastus* given by Breimer and Macurda (1972). The number of anal deltoids is unknown in *H.(?) benniei* and the form of the aboral part of the deltoid body is different from the North American species of *Hadroblastus*. Lack of information on the anal deltoids would appear to be the only character precluding definite assignment to *Hadroblastus*. An incomplete blastoid from beds of C₂S age near Dublin, Ireland was questionably identified as *Hadroblastus* sp.? by Breimer and Macurda (1972). If assignable to *Hadroblastus*, *H.(?) benniei* would represent the youngest occurrence of the genus, being D₂ in age.

Acknowledgements. I wish to thank Dr. C. D. Waterston (Royal Scottish Museum, Edinburgh) for the loan of specimens from the Wright Collection and Drs. R. P. S. Jefferies and H. Owen, British Museum (Natural History), London for access to collections in their care. Part of this research was conducted under National Science Foundation Grant GB-5802. Scanning electron microscopy was conducted in the Scanning Electron Microscope Laboratory, University of Michigan, Dr. W. C. Bigelow, Director.

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Cover: A Middle Jurassic megaspore, *Minerisporites richardsoni* (Murray) Potonié, from Oxfordshire (×350, S.E.M. by T. M. Windle).

EVOLUTION IN CARNIVOROUS MAMMALS

by R. J. G. SAVAGE

Nineteenth Annual Address, delivered 17 March 1976

In tauros Libyci ruunt leones;
Non sunt papilionibus molesti.

(In Africa lions attack bulls;
they do not molest butterflies.) *Martial*

ABSTRACT. Carnivorous mammals are identified on the basis of their carnassial dentition and their predatory preference for vertebrates. Jurassic pantotheres possess a dentition from which arose both carnivore and herbivore specializations. The changes towards carnivorous feeding involved emphasis on the cutting functions of the cheek teeth, with corresponding reduction of the crushing activities. A carnivorous mode of living evolved twice among the marsupials (borhyaenids in South America and some dasyurids in Australia) and twice among the placentals (Creodonta and Carnivora). Characteristics of the post-cranial skeleton in carnivores are mentioned. Features of the jaw mechanics, the brain, and the senses (smell, sight, and hearing) are discussed. Specializations of sabre-like canines and crushing premolars are discussed. The form and function of the carnassial dentition and its evolution are analysed.

THE evolutionary history of elephants and horses is well documented yet, despite a reasonable fossil record, there is surprisingly little information readily available on the evolutionary history of carnivores. Detailed taxonomic accounts of faunas and phylogenetic studies of families abound, but the literature on functional aspects of carnivore evolution is meagre. Three papers are outstanding exceptions to this generalization: Denison (1938) on creodonts, Simpson (1941) on sabre-toothed carnivores, and Crusafont and Truyols (1956) on the evolution of carnassial teeth.

THE LIVING CARNIVORE

Let us examine a lion as a living representative of one of the peaks of carnivore evolution and see what distinguishes it from the herbivorous gazelles it preys upon and also from its shrew-like ancestors of the earliest Tertiary. What in other words, starting from a shrew, would be the modifications required to produce a lion?

To earn a living as a carnivore, the first essential is to locate your victim—before he locates you. This means having very acute sensory receptors (vision, hearing, and smell), and a first-class brain to integrate rapidly and efficiently and to analyse the information. In the lion, as often in carnivores, sight is the most important sense, with the eyes set well forward giving stereoscopy. Hypermetropic vision, and ability to judge distances accurately, enable the lion to locate its victim precisely. The next move is to creep up close stealthily; ability to move silently close to the ground and to take maximum advantage of cover is essential. Then, to make contact, a burst of very high speed is needed; long legs with muscles aligned to give maximum mechanical advantages for speed and physiologically adapted for rapid

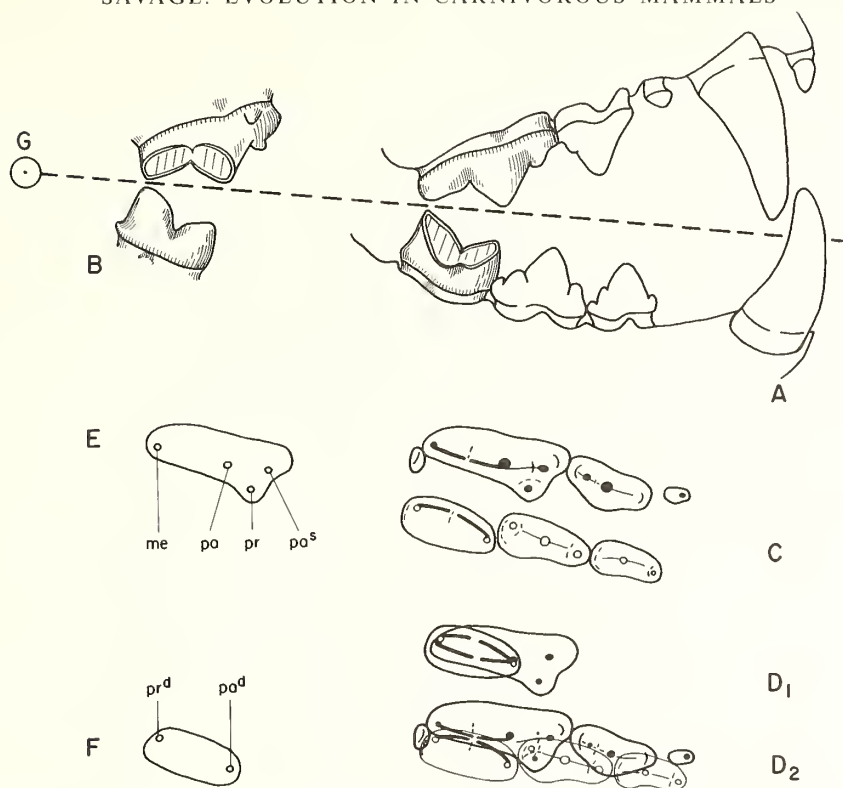
contractions, ensure success. The attack on the victim must be swift to be effective; usually the gazelle is thrown off balance with a sideways crash which enables the lion to plunge its canine teeth into the throat region while holding the prey down with the claws of its forepaws. The carnivore will then rip open the carcass, using incisors and canines. The meat is torn off and cut into chunks, with the powerful closing muscles of the jaws operating the scissor-like carnassial blades of the cheek teeth. But even with all these refinements, the lion has on average only about a one in five chance of success; it is clearly not a game for amateurs.

There is no sharp distinction between insectivore and carnivore. Neither is a single natural order of mammals; they reflect modes of living. There are some ten orders of mammals that are basically insectivorous, and about twenty orders that are essentially herbivorous. There remain only two that are fundamentally carnivorous, the Creodonta and the Carnivora, with the Marsupialia evolving two carnivorous stocks from insectivorous ancestors. In this review we shall omit the Cetacea, which would make the fourth carnivorous order; they are so specialized as marine aquatic mammals that the carnivore specializations are relatively secondary and quite unlike those of land mammals.

The two prime essentials of a carnivore are that its diet include a substantial proportion of vertebrates, and that it possesses a carnassial dentition. By specifying vertebrates, we can eliminate the insectivores, though this also leaves out animals like the mollusc-feeding sea otter *Enhydra*, and, of course, those members of the order Carnivora which have become secondarily herbivorous, such as the pandas and some of the bears. A few herbivores have produced omnivorous stocks that are partially carnivorous; for example, some pigs and the extinct mesonychids have large incisor or canine tusks and may supplement their diet with animal food, but they never achieve a carnassial dentition which is the hallmark of a truly carnivorous land mammal. When one or more pairs of upper and lower cheek teeth develop a blade structure, such that on closing the jaws these blades pass over each other like scissor blades, this is spoken of as carnassial specialization (text-fig. 1). Slicing teeth develop in some herbivores, e.g. pyrotheres, deinotheres, barytheres, and macropodids; these are always on transverse lophs, extend along all or most of the cheek dentition, and are not self-sharpening, so that with wear the dentition becomes flattened. The extinct marsupial *Thylacoleo* is a puzzling exception; it has a 'carnassial' specialization, but otherwise retains many phalanger characters, which makes it difficult to interpret it as anything but a specialized herbivore (Gill 1954).

THE ANCESTRY OF CARNIVOROUS MAMMALS

The mammals of the Jurassic were essentially small insectivorous beasts and probably nocturnal. Multituberculates were the exception in being specialized rodent-like herbivores, but an aberrant sideline destined to leave no descendants. By mid Cretaceous times we can recognize, in the main stream of mammalian evolution, a fork into marsupial and placental stocks. While this cleft is based fundamentally on reproductive differences, some dental characters enable us to detect it; for example, the presence of certain styler cusps on the outer margin of the upper molars is a marsupial feature unknown in placentals. Though our knowledge is as yet very



TEXT-FIG. 1. Views of the carnassial dentition of *Felis*. A, lateral view, P⁴ and M₁ in relief; B, internal view of P⁴ and M₁; C, occlusal view of upper and lower cheek dentition, carnassial blades in heavy lines; D₁, carnassial teeth at beginning of occlusion; D₂, cheek dentition in full occlusion; E, cusps of P⁴: *me* metacone, *pa* paracone, *pa*^s parastyle, *pr* protocone; F, cusps of M₁ = *pa*^d paraconid, *pr*^d protoconid; G, position of glenoid jaw articulation with respect to A.

slender, there is evidence that during mid Cretaceous times there were considerable floral changes. Table 1 (after Hughes 1976) shows the proportion of flowering plants (angiosperms) to other megaplants. In the earliest Cretaceous the gymnosperms and pteridophytes share the total in equal proportions. By latest Cretaceous the angiosperms have taken over 90% of the flora, the number of gymnosperms has dropped dramatically, and although the ferns have actually increased in species numbers, their proportion of the total flora is drastically reduced. Angiosperms arose in the early Cretaceous and rapidly expanded; this must surely have led to a diversification

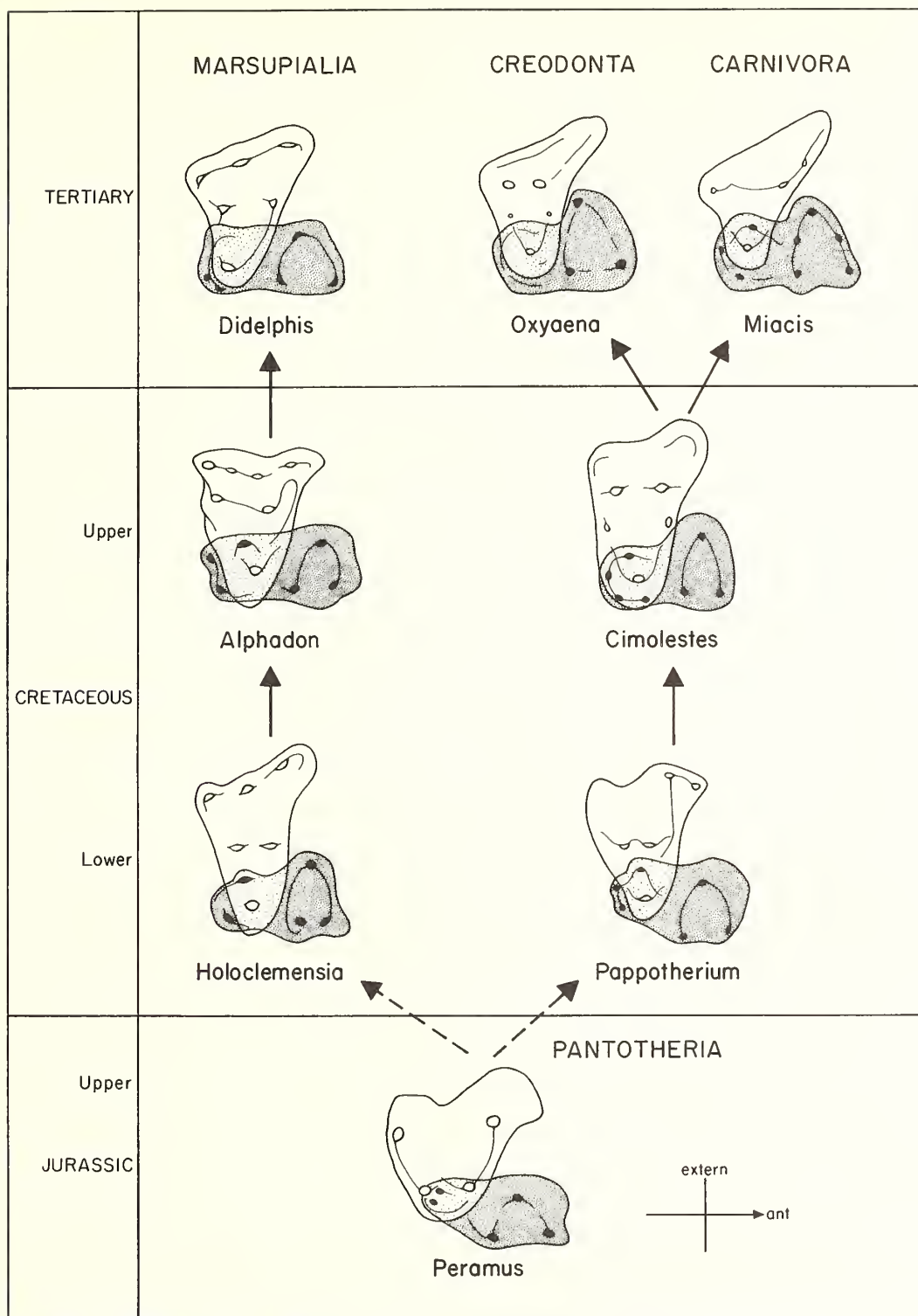
TABLE 1. Estimated number of megaplant species (after Hughes 1976).

	Pteridophyte	%	Gymnosperm	%	Angiosperm	%
Recent	10 000	3.4	640	0.2	286 000	96.4
Latest Cretaceous	2 000	9	500	2	20 000	89
Earliest Cretaceous	1 500	50	1 500	50	0	0

of the insect fauna. The Cretaceous insect record is, however, very poor, and the most that can be said is that when good faunas are next seen, in early Tertiary, they show a major advance on Jurassic faunas, with a much greater diversity (Crowson *et al.* 1967). Insectivorous mammals usually include fruit, nuts, and berries in their diet; the much greater range of these, and probably also of insects, in the Late Cretaceous is likely to have been a critical factor in mammalian radiation.

By Late Cretaceous times the mammals show considerable diversity, though still largely within the same niches of small sized insectivorous stocks. Within these faunas, however, we can detect the beginnings of several orders of Tertiary mammals, in particular the early trends towards herbivore and carnivore lineages. By terminal Cretaceous and earliest Tertiary, these lineages became distinct as the mammals invaded the niches left vacant by the dinosaur extinctions. The detailed stages of the take over are not known, though many speculations have been made. Small mammals could compete successfully with reptiles throughout the Mesozoic only by occupying niches unavailable to reptiles. Mammalian endothermy, even if relatively inefficient, would have given them an advantage over reptiles in temperate climates (and temperate climate microniches) enabling them to feed at night, so long as they could hide during the day from the predatory lizards and dinosaurs. The need to hide imposed size limitations on the mammals; furthermore, it is not efficient for an insectivorous mammal to grow large unless bulk food is available. Insects in bulk only became possible food sources when colonial ants and termites evolved, probably in the Oligocene. Mammalian eyes are primarily designed for nocturnal vision, since the receptor cells are predominantly rods; they secondarily became adapted for diurnal vision by increasing the numbers of cones. Here again, mammals would have the advantage over the smaller dinosaurs, which may have been endothermic but are likely to have had poor night vision. When the diurnal niches became available in the terminal Cretaceous, the mammals were ready to invade them. Gradual improvements in their physiology, in particular temperature control and metabolic rates, enabled them to increase in size and to acquire specialized trophic preferences. Tooth adaptations evolved in the herbivore lineages to crush food, and in the carnivores to cut it into chunks small enough to swallow.

Text-fig. 2 illustrates trends in mammalian molar teeth during the Mesozoic. While named genera are chosen as examples, this does not imply that they are on direct lines of descent, only that we can trace likely lineages from the stocks to which they belong. In the Jurassic, a pantothere such as *Peramus* has a cheek dentition with primitive tribosphenic pattern, that is to say upper and lower wedge-shaped triangular teeth that cut against each other. A detailed and lucid analysis of the functional principles of tribosphenic molars is to be found in Crompton and Sitalumsden (1970). *Peramus* has a good insectivorous dentition, capable of cutting up small and relatively soft food. From the Early Cretaceous of Texas come *Holoclemensia* and *Pappotherium*, which probably respectively belong to primitive marsupial and placental stocks. Their teeth are rather similar and functionally show a considerable change from those of *Peramus*; they have acquired a protocone cusp on the inner side of the upper molar, and a talonid or basin has developed in the lower molar to receive the impact of the protocone on occlusion. Thus a crushing action is now added to the slicing action of the Jurassic mammals. By the Late



TEXT-FIG. 2. Evolution of carnassial teeth; lower molars stippled and showing the overlap of upper and lower teeth in full occlusion.

Cretaceous, the marsupial *Alphadon* and the placental insectivore *Cimolestes* are in their dental pattern almost unchanged descendants; the marsupials are distinguished by having a broad styler shelf on the labial side. The ratio of crushing/slicing varies in different taxa. Crompton and Hiimae (1970) have estimated that in the living opossum *Didelphis*, which differs little from the Late Cretaceous marsupials, 60% of the chewing time is spent on pulping food with their sharp cusps and 40% on cutting.

In the early Tertiary, both marsupial and placental stocks evolved carnivorous lineages (see Table 2 and text-fig. 18). From didelphid marsupials in South America

TABLE 2. Families of terrestrial carnivorous mammals.

Orders	Families	Stratigraphic range	Geographic distribution	Extinct genera	Living genera	Total no. of genera
MARSUPIALIA	(Didelphidae)	L. Cret.-Rec.	N. & S. Am., Eu.	(1)		(1)
	Borhyaenidae	U. Pal.-Plio.	S. Am.	25	-	25
	(Dasyuridae)	U. Oligo.-Rec.	Australia	2	2	4
	(Phalangeridae)	Mio.-Rec.	Australia	(1)	-	(1)
	Total MARSUPIALIA			29	2	31
CREODONTA	Oxyaenidae	U. Pal.-U. Eo.	N. Am., Eu., As.	10	-	10
	Hyaenodontidae	L. Eo.-U. Mio.	N. Am., Eu., As., Af.	35	-	35
	Total CREODONTA			45	-	45
CARNIVORA	Miacidae	M. Pal.-L. Oligo.	N. Am., Eu., As.	16	-	16
	Amphicyonidae	U. Eo.-U. Mio.	N. Am., Eu., As., Af.	29	-	29
	Canidae	M. Oligo.-Rec.	N. & S. Am., Eu., As., Af.	22	13	35
	Ursidae	U. Eo.-Rec.	N. & S. Am., Eu., As., Af.	22	6	28
	Procyonidae	L. Mio.-Rec.	N. & S. Am., Eu., As., Af.	14	8	22
	Mustelidae	L. Oligo.-Rec.	N. & S. Am., Eu., As., Af.	65	29	94
	Viverridae	U. Eo.-Rec.	Eu., As., Af.	11	36	47
	Hyaenidae	M. Mio.-Rec.	Eu., As., Af.	8	3	11
	Felidae	U. Eo.-Rec.	N. & S. Am., Eu., As., Af.	31	3	34
	Total CARNIVORA			218	98	316
Total MARSUPIALIA, CREODONTA and CARNIVORA				292	100	392

Note. Marsupial families in brackets are mainly non-carnivorous, and only the carnivorous genera are counted.

arose the borhyaenids, with twelve known genera ranging from Palaeocene to Pliocene times. Within the dasyurid marsupials of Australia arose carnivorous taxa such as *Sarcophilus* (native cat) and *Thylacinus* (native wolf); we know dasyurid history only back to the Miocene, though its origins are certainly earlier. From placental insectivores two carnivorous lineages differentiated during the Palaeocene, the Creodonta and the Carnivora (*sensu stricto*).

The classification of the higher categories of placental carnivores has undergone major changes over the past decade, and no widely accepted grouping has yet emerged. The degree of change is apparent when the classification of Simpson (1945), which has for long been the accepted classification, is compared with the one used here (Table 3).

The proposed grouping is not as radical as might at first sight appear; it is largely a tidying-up operation following detailed studies on some groups. For almost a

decade it has been accepted that the Arctocyonidae and Mesonychidae are condylarths and not creodonts; they lack carnassial specializations and have developed crushing dentitions. The only remaining creodonts are the truly carnivorous oxyaenids and hyaenodontids. The miacids are the accepted ancestral stock of living carnivores and, since both creodonts and miacids can be traced independently back to an insectivore ancestry in the Palaeocene, I consider that the Creodonta and Carnivora should have equal rank as orders. Savage (1957) suggested that the pinnipeds were probably diphyletic. This has been followed up by other authors, and new discoveries, especially that of the new sub-family Enaliarctinae (Mitchell and Tedford 1973), have added greatly to our knowledge of aquatic lineages. Unfortunately the phocids have a poor fossil record compared with the otariids; nevertheless it seems likely that the otariids arose via enaliarctines from canoid ancestors, with odobenines as a side line, while the phocids arose from a mustelid ancestor. Acceptance of this diphyletic origin means the disappearance of the pinnipeds, and so also the need for the term fissiped. I have grouped the carnivore families into five superfamilies; this is a fairly orthodox classification more like that of Gregory and Hellman (1939) than that of Simpson (1945). I cannot identify a mustelid ancestor among the canoids, and the family seems more likely to have arisen directly from a miacid ancestor. It appears equally likely that felids and viverrids have independent origins from miacids. The Eocene faunas of carnivores form a complex of taxa which it is sometimes difficult to assign with certainty to living families.

TABLE 3. Classifications of carnivores.

SIMPSON 1945	
Superorder FERA	
Order CARNIVORA	
Suborder CREODONTA	
Superfamily Arctocyonoidea	(Arctocyonidae)
Mesonychoidea	(Mesonychidae)
Oxyaenoidea	(Oxyaenidae, Hyaenodontidae)
Suborder FISSIPEDA	
Superfamily Miacioidea	(Miacidae)
Canioidea	(Canidae, Ursidae, Procyonidae, Mustelidae)
Feloidea	(Viverridae, Hyaenidae, Felidae)
Suborder PINNIPEDIA	(Semantoridae, Otariidae, Odobenidae, Phocidae)
SAVAGE 1977	
Superorder FERA	
Order CREODONTA	
Superfamily Oxyaenoidea	(Oxyaenidae, Hyaenodontidae)
Order CARNIVORA	
Superfamily Miacoidea	(Miacidae)
Canioidea	(Amphicyonidae, Canidae, Ursidae, Procyonidae, Otariidae)
Musteloidea	(Mustelidae, Phocidae)
Viverroidea	(Viverridae, Hyaenidae)
Feloidea	(Felidae)

THE GEOMETRY OF THE FOSSIL RECORD

There are almost 1000 genera of living mammals, and in trophic terms they can be grouped thus: carnivores 10%, insectivores 23%, herbivores 14%, omnivores 9%, gnawers 38%, and aquatic taxa 6%. Leaving aside the aquatic forms, carnivores today make up about 11% of all land mammal genera. Taking the fossil record into account, we know in all about 3000 mammalian genera, and of these 14% are carnivores; this apparent rise is in part due to smaller mammals (rodents and insectivores) being less well represented in the fossil record. In Table 4 we see an analysis of Tertiary mammal faunas in North America, Africa, and South America. The North American record is good at all periods and shows that carnivores have ranged from 16 to 32% (mean 22%). The African record is much less complete and shows carnivores with a slightly lower range, 12–28% (mean 18%). The South American record yields figures of 3–9% (mean 6%); this much lower range may in part be due to inadequate sampling, but also to the carnivore niche being in part occupied by the large phororhachid birds. If these birds are taken into account, the range for carnivores becomes 3–13% (mean 9%).

TABLE 4. Percentages of carnivores in Cenozoic land mammal faunas.

	North America			Africa		
	Creodonta	Carnivora	Total	Creodonta	Carnivora	Total
Pleistocene	—	21.0	21.0	—	16.0	16.0
Pliocene	—	23.7	23.7	—	28.0	28.0
Miocene	—	31.6	31.6	6.0	6.0	12.0
Oligocene	2.6	13.2	15.8	16.0	—	16.0
Eocene	14.0	5.3	19.3	17.3	—	17.3
Palaeocene	18.4	2.6	21.0	—	—	—

	South America			
	Marsupial carnivores	Placental carnivores	Phororhachoid birds	Total carnivores
Pleistocene	—	9.1	2.4	11.5
Pliocene	4.5	1.8	3.7	10.0
Miocene	6.3	—	7.0	13.3
Oligocene	6.3	—	5.2	11.5
Eocene	3.9	—	—	3.9
Palaeocene	2.6	—	—	2.6

Table 4 also illustrates how the Carnivora gradually replaced the Creodonta in North America, and similarly in Africa, though here the creodonts persisted until the Late Miocene. In South America the early Tertiary carnivores were marsupials; these were supplemented in the Oligocene by phororhachid birds, and finally the placental carnivores invaded that continent in the Pliocene and displaced both native stocks.

Considering now the biomass relationships, the standing crop ratio of predators to prey is around 2–3%; for example, the Ngorongoro crater in Tanzania supports around 25 000 large herbivores and around 500 large carnivores. These ratios are

fairly constant for endotherms (Bakker 1972); in a Pliocene mammal community in Nebraska analysed by Voorhies (1969), the ratio was around 3%.

Reasonably complete skeletal remains of carnivores are rare, for example the skeletons of only three borhyaenids and six creodonts have been reassembled. A fair number of skulls of most families are preserved, but the majority of taxa are known only from mandibular and maxillary fragments with incomplete dentitions. The Palaeocene record is very weak, with Europe and North America the only continents from which adequate faunas are known throughout the Tertiary.

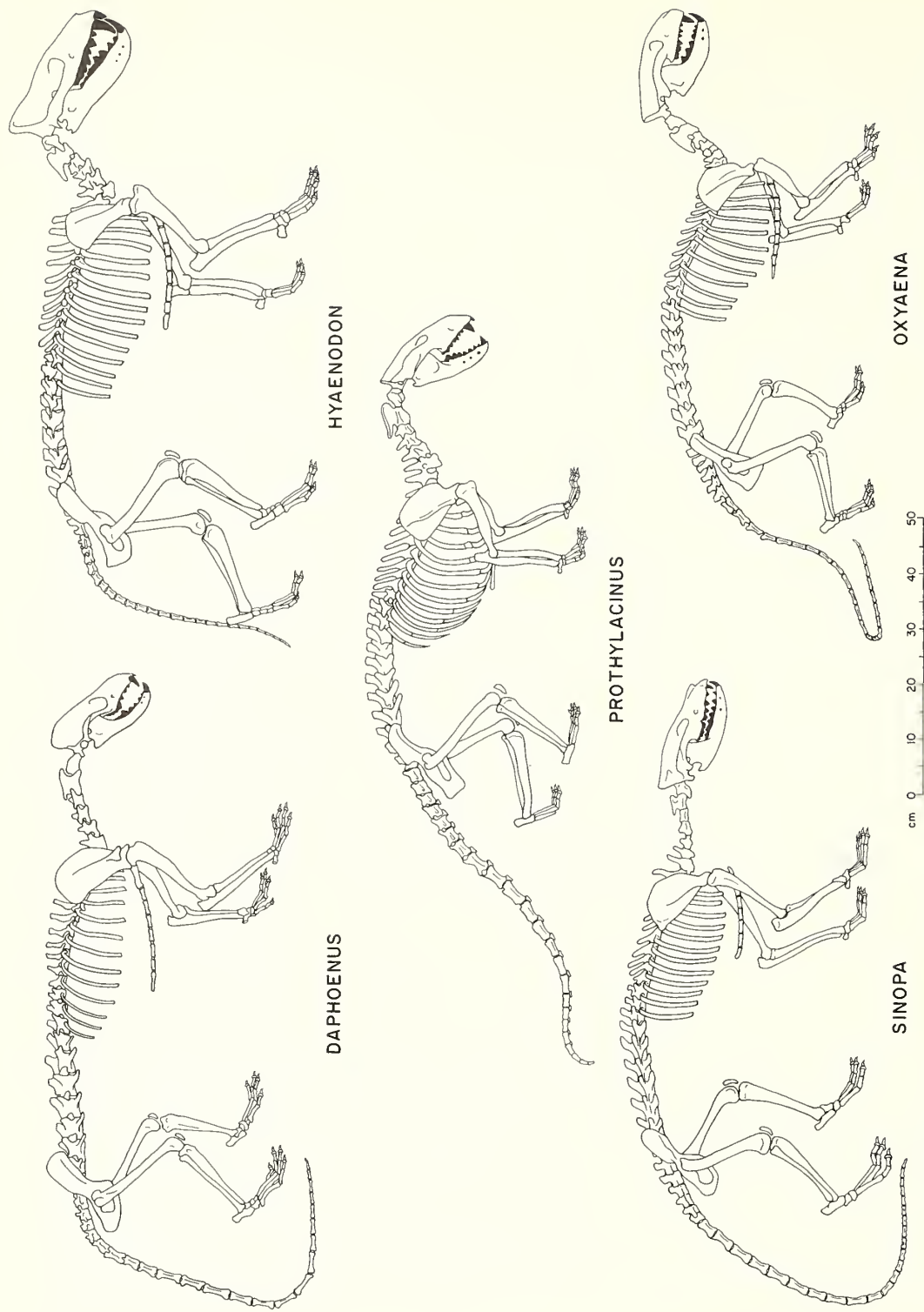
Carnivores have a greater size range than that found in any other mammalian order; they range from a weasel of around 50 gm to a Kodiak bear of around 800 kg. The weasel is about ten times larger than the smallest shrew; the largest bear is about a tenth the weight of an elephant. All small carnivores have to compete with the predatory birds, and the majority of carnivores are small to medium sized. Two-thirds of all living carnivore genera belong to two families, the Viverridae and Mustelidae. Omitting the aquatic otters, the mean weight for mustelids is 4.3 kg and for viverrids is 3.6 kg; rodents and insectivores are major items in their diets. The weasel can cope with small rodents such as mice and rats, but if it were any smaller the range of prey would presumably be too restricted and the energy expended in obtaining small food packages would exceed the intake. At the other end of the scale, carnivores cannot afford to become too large, as they pay a heavy price for this in loss of speed. In order to tackle prey much larger than themselves, carnivores hunt in groups, making use of their superior intelligence to overcome other shortcomings.

The largest known fossil carnivore is the hyaenodont *Megistotherium*. The skull is about twice the size of that of a large bear—and bears are omnivorous rather than truly carnivorous. It is possible that *Megistotherium* was a carrion feeder; it appears from the dentition to have been capable of crushing bone and cutting flesh (Savage 1973). The weight of *Megistotherium* is difficult to estimate as hyaenodonts tend to have heads which are large in proportion to their bodies. In 1973 I suggested that it might have weighed around 880 kg; this is little more than a guess, it could have been half or twice that figure.

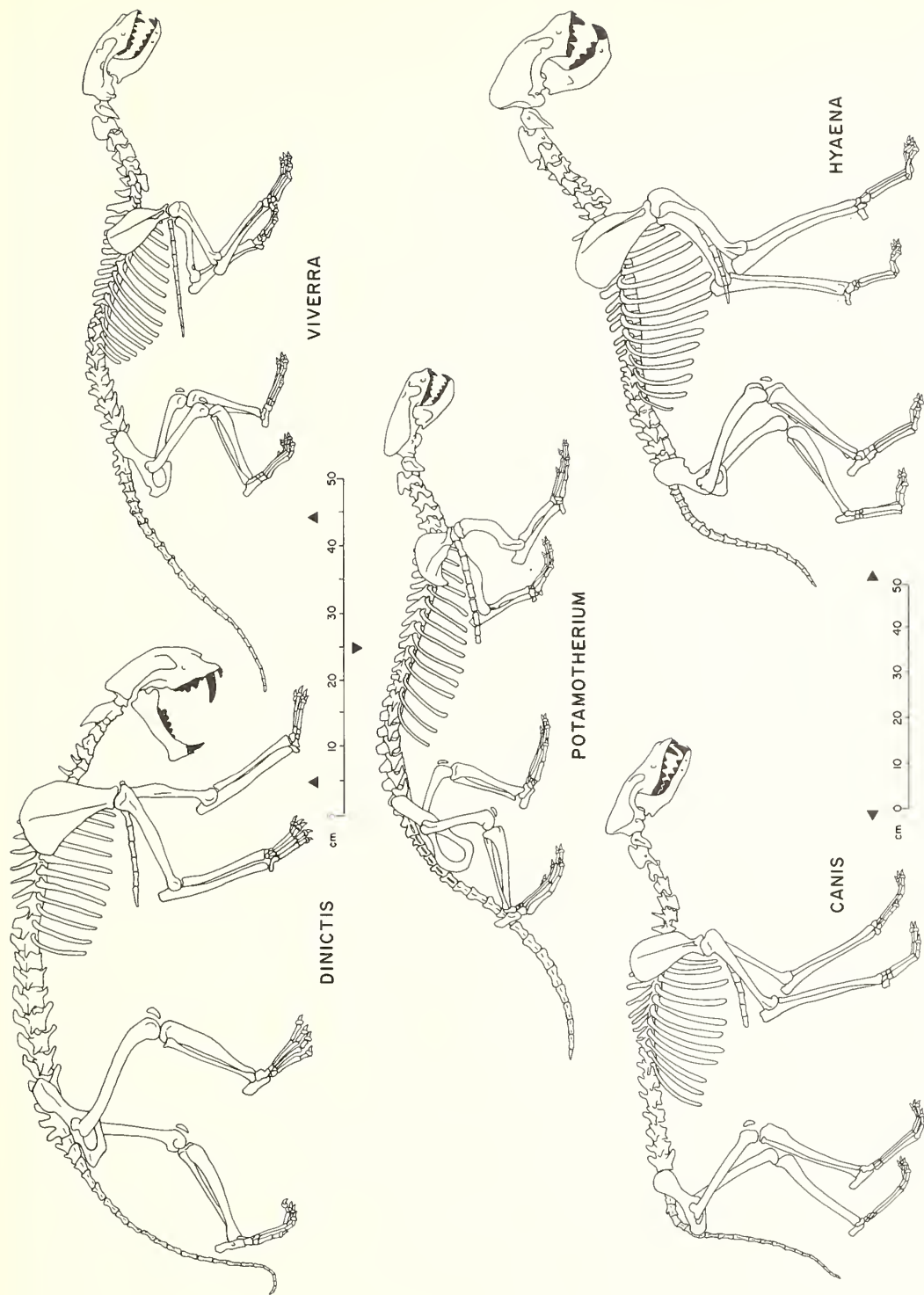
THE POSTCRANIAL SKELETON

The postcranial skeleton of carnivores (text-figs. 3 and 4), excluding the fully aquatic pinnipeds, is less modified than that seen in many other mammals. Nevertheless, there are many differences within carnivores which also show many advances from the primitive insectivore skeleton.

Stromer (1902), in a large monograph on the carnivore vertebral column, stated that the morphological details of the individual vertebrae exhibit no important features consistently correlated with major phyla and therefore are of little systematic importance; they reflect function and not relationship. Hildebrand (1961), in a paper on the body proportions of marsupials, noted that marsupials have a greater variation in postcranial proportions than is found in placental mammals in general and



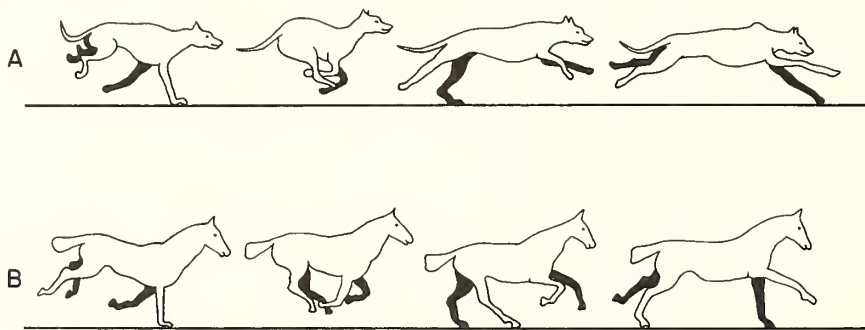
TEXT-FIG. 3. Skeletal reconstructions: borhyaenid *Prothylacinus* (after Sinclair 1906); creodonts *Sinopa* (after Matthew 1906), *Oxyaena* (after Osborn 1900), and *Hyaenodon* (after Scott and Jepsen 1936); amphicyonid *Daphoenus* (after Scott and Jepsen 1936).



TEXT-FIG. 4. Skeletal reconstructions: mustelid *Potamotherium* (after Savage 1957); canid *Canis dirus* (after Merriam 1912); viverrid *Viverra* and hyaenid *Hyæna* (after Blainville 1864); felid *Dinictis* (after Scott and Jepsen 1936).

in canids in particular. Within the didelphids there is some correlation between body proportions and habit for aquatic and riparian species, but not for arboreal, semi-arboreal, or terrestrial species. In another paper, Hildebrand (1954) remarked that in the ungulate skeleton nearly every bone has been profoundly modified to adapt the animals for running; although some canids can overtake fast ungulates, none of their bones is so strikingly altered in response to cursorial habit. Nevertheless, most skeletal differences among canids can be attributed to variation in the degree of cursorial specialization.

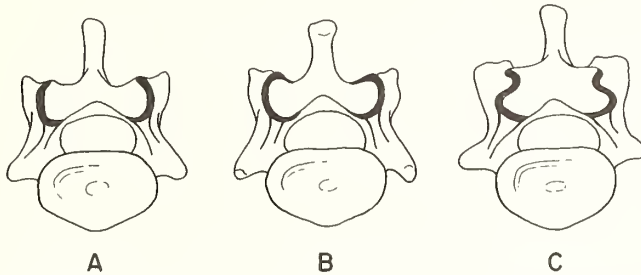
In carnivores, the prime essentials of the postcranial skeleton are strength, flexibility, and adaptability. Insectivores are scurrying creatures, carnivores are usually cursorial beasts. The carnivores need to move slowly and rapidly, to crouch down and stand up full stretch, to turn rapidly, and sometimes to climb, dig, or swim, and to use the limbs to clasp struggling prey. Most carnivores can achieve a galloping gait, a gait in which all four feet are off the ground simultaneously. As Smith and Savage (1956) have shown, the carnivore gallop is very different from that of herbivores. In carnivores the vertebral column and limbs are flexed, then unfolded like a spring to give the animal vertical and horizontal thrust, projecting it through a parabola with a long airborne phase (text-fig. 5A). Small herbivores may adopt the carnivore method of galloping but very large graviportal forms do not gallop, or do so only rarely. The majority of medium-sized herbivores gallop with a stiff vertebral column that scarcely rises, and most of the energy is expended in swinging the limbs (text-fig. 5B).



TEXT-FIG. 5. Sequence of phases in the gallop of a dog and a horse (after Muybridge 1899).

The vertebrae of carnivores, like the limb bones, are robust and well sculpted for the origins and insertions of muscles. The neural spines of the thoracic vertebrae are long, accommodating the origins of the strongly developed neck muscles. There is little variation in the number of presacral vertebrae, usually 27 ± 1 . The neck does not vary greatly in length, but the atlas is often diagnostic to family and sometimes generic level. The position of the vertebralarterial canal on the atlas has characteristic patterns and there is considerable variation in the shape of the wings; these are, for example, narrow and sagittally elongate in sabre-tooth cats. While there are usually 20 thoracic and lumbar vertebrae in carnivores, the proportions vary. The lumbar

vary from 4 to 7, though 5 or 6 is normal in both creodonts and living carnivores; the arboreal pandas often have only 4 lumbers. Savage (1957) demonstrated that the zygapophysial articulations of the thoracic vertebrae are orientated to allow great freedom of movement, and in particular to allow the anterior part of the body to twist relative to the posterior. This twisting ability is a uniquely mammalian characteristic, but is poorly developed in herbivores as compared to carnivores. The longer the thoracic region and the more posterior the anticlinal vertebra, the greater is the degree of flexibility. Creodonts have in general a less flexible column than living carnivores. The creodont lumbar vertebrae have tight articulations and very little freedom of movement; this is seen most markedly in *Patriofelis*, which has sigmoidal-shaped zygapophyses (text-fig. 6). Tail lengths are highly variable,



TEXT-FIG. 6. Posterior view of lumbar vertebrae, showing extent of articulatory surface of posterior zygapophyses in heavy line. A, typical of Carnivora; B, typical of Creodonta; C, as found in *Patriofelis* (after Denison 1938).

even within a species, as is common in mammals, but on the whole they tend to be long. All creodonts and marsupial carnivores have long tails; among living carnivores only bears, giant pandas, and a few hyaenas and cats have notably short tails—and of these bears are omnivorous and giant pandas herbivorous. The cats with short tails are the lynxes and some sabre-toothed cats. Lynxes tend to be slow movers, often living in forests, where they climb in trees and feed on rabbits and hares. The sabre-toothed cat *Smilodon*, with its rather short hind legs, may not have been a fast runner. The marsupial sabre-tooth *Thylacosmilus*, however, appears to have had a reasonably long tail. Tails are used for balance when changing direction at high speed, for swimming in otters, and other occasional uses include its use as a prehensile organ for climbing as in procyonids. In small species, a bushy tail coiled round the body is important in keeping the animal warm.

Much more variation is seen in the girdles and limbs than in the vertebral column. The scapula is usually fairly broad, with the supraspinous fossa often equal to or even larger than the infraspinous fossa; in ungulates the supraspinous fossa tends to become much the smaller. The scapular spine, acromion, and metacromion are usually well developed; they serve for the origins of muscles which abduct the limb, and in ungulates, with their specializations towards antero-posterior limb movements, these processes are reduced. The clavicle is vestigial or absent, as would be expected. In the pelvis the ilium and ischiopubis are usually of equal length; in

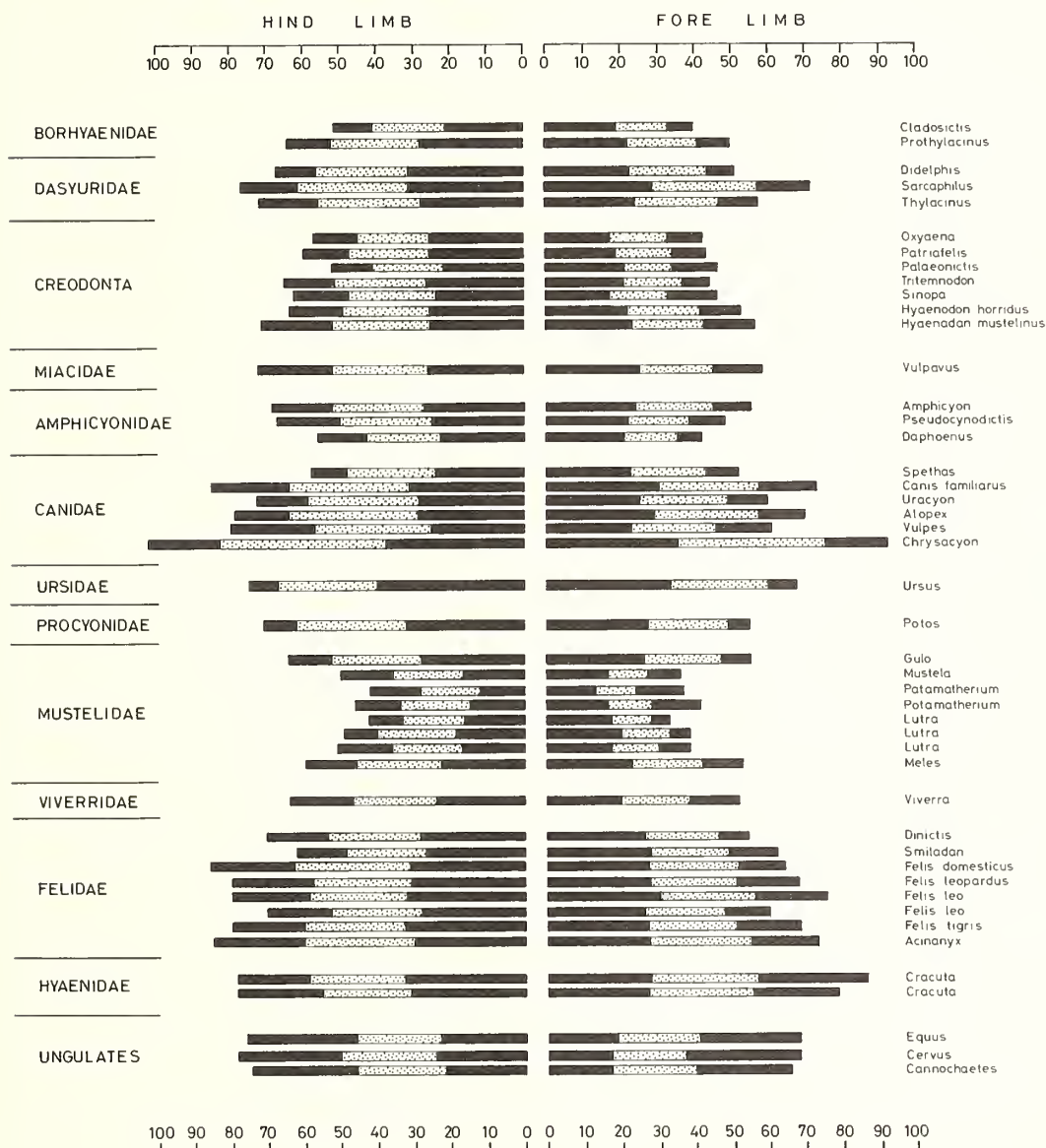
aquatic carnivores the ilium is much shortened and the ischiopubis lengthened, while the opposite trend is seen in ungulates. Smith and Savage (1956) demonstrated that this difference was explicable as an adaptation to powerful limb movements in carnivores and rapid movements in ungulates. The ilium in creodonts is usually expanded dorsally and has a strong longitudinal keel. Since creodonts have three sacral vertebrae as in living carnivores, the heavier ilium was not for greater pelvic rigidity, but rather for more massive gluteal musculature. This, combined with the development in creodonts of a third trochanter on the femur, is indicative of the strong abduction capabilities of the limb.

In carnivores the hind limb is used almost solely for locomotion, but the fore limb has many additional uses—climbing, digging, grooming, tearing, and holding prey. Limbs can never be as specialized as in herbivores, where they are used almost exclusively for one mode of locomotion. The proportions of the limb segments have attracted the attention of many authors, but it is still difficult to provide more than broad generalizations. In order to compare both relative length and proportions of the limbs, I have compiled a graph (Table 5) where the limbs and their segments are expressed as a percentage of the vertebral column length, measured from the atlas to the last lumbar vertebra. In the less-specialized carnivores (e.g. *Mustela* or *Viverra*) the three segments of the limb become progressively shorter distally. In cursorial ungulates (e.g. *Equus* or *Connochaetes*) the reverse is true. In cursorial carnivores the foot is always the shortest element and the other two segments approach equality in length. Hildebrand (1961) concluded that only aquatic adaptations (all segments short) were clearly differentiated on limb proportions. Arboreal and fossorial forms also tend to have short limbs. Hind limbs are usually about 10% longer than the fore limbs; hyaenas are the exception with fore limbs equal to, or longer than, the hind. We might define short-legged carnivores as those whose fore limbs are 40% or less of the vertebral column, and the hind limbs 50% or less; this would include the otters, some *Mustela* species, and the borhyaenid *Cladosictis*. If we define long-legged as 70% or more for the fore limbs and 80% or more for the hind limbs, then the candidates are some species of *Felis* and *Canis*, together with *Acinonyx* and *Chrysocyon*; all these are cursorial and mostly high-speed runners. But *Chrysocyon* is not a particularly fast runner; increase in speed is bought at the expense of power. The very long legs of *Chrysocyon* are an adaptation to living in the long pampas grass.

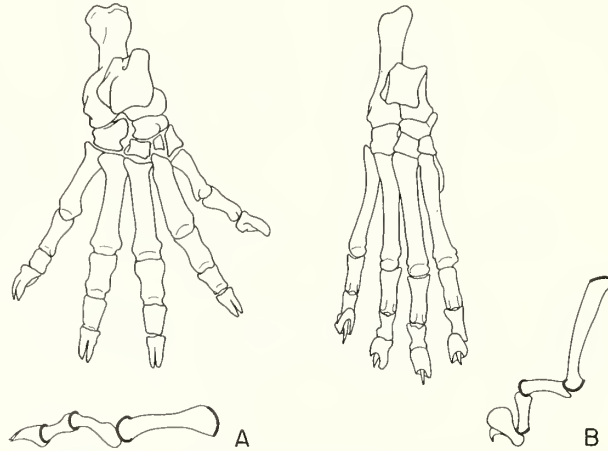
From our knowledge of locomotion in living carnivores, we can look at the fossils and make comparisons on limb proportions. The borhyaenid *Cladosictis* has limb proportions almost identical with those of the living otter *Lutra*, and both animals are of similar size. *Prothylacinus* has the size and proportions of the living wolverine *Gulo*. Oxyaenids and provirerrines all have shortish limbs, especially the fore limbs; it seems probable that these are primitive character traits rather than aquatic specializations. *Hyaenodon* has longer limbs, though still shorter than those of living cursorial carnivores. The amphicyonids vary from fairly lightly-built forms to very large bear-like varieties.

There are all gradations between plantigrade and digitigrade. On the whole the more primitive carnivores, arboreal, and slower-moving animals, have plantigrade feet, while all cursorial types have digitigrade feet, or are capable of achieving

TABLE 5. Limb proportions of carnivorous mammals, shown as percentages of vertebral column length (atlas to last lumbar vertebra), with those of three ungulates for comparison. First joint (femur or humerus) and pes shown in black. Second joint (tibia-fibula or ulna-radius) stippled.



digitigrade posture, which considerably lengthens the limb and so adds to the mechanical advantage of the lever system. Borhyaenids and early creodonts were plantigrade, but later hyaenodontids were fully digitigrade (text-fig. 7). Plantigrade taxa have short, broad, and widely spread metapodials; in digitigrade taxa the metapodials are long and slender and held close together with strong tendons to give support when the foot is elevated. The scapho-lunar bones never fuse in creodonts, as they do in living carnivores; the unfused condition might have given greater freedom of movement in the wrist joint. Living carnivores have lost this



TEXT-FIG. 7. Right pes of A, plantigrade creodont *Patriofelis* (after Denison 1938) and B, digitigrade carnivore *Felis* (after Merriam and Stock 1932); each pes shown with one digit in lateral view, the articular facets emphasized with heavy line.

freedom but, in compensation, the digitigrade foot is more firmly supported. The carnivore astragalus always has a good pulley articulation with the tibia, and in creodonts the astragalar foramen is always present. There are never more than four functional digits, with the first variously reduced; in some arboreal species it may be partially opposed.

The ungual phalanges of creodonts are fissured; while this serves to distinguish them from living carnivores, it is not a unique character—they also occur in living condylarths, pangolins, and chalicotheres. Most felids and a few viverrids have evolved retractile claws; this serves to prevent the claws from becoming blunt in walking, so that they retain their maximum sharpness for tearing prey.

THE BRAIN AND THE SENSES

Until about a decade ago, Edinger's (1929) paper contained almost all that was known of fossil carnivore brains. Piveteau (1961) illustrated thirteen genera, with anatomical notes commenting on the patterns of the sulci and gyri; his conclusion was that larger and more Recent brains tend to be more fissured and more complex.

More recently Jerison and Radinsky have in different ways made significant contributions. Jerison (1961, 1973) took a broad approach to the problems of brain evolution in vertebrates and concentrated mainly on characteristics of brain weight to body weight ratios. In amniotes the brain weight (E) increases as the two-thirds power of the body weight (P), that is $E = kP^{0.66}$ where k is a constant. Jerison also made use of an encephalization quotient (EQ), which is the ratio of the actual measured brain size to the expected brain size in an 'average' mammal of the same body weight.

The data for carnivores in Table 6 is extracted from Jerison (1973) with the addition of some original data. The estimates of brain weight and body weight can rarely

TABLE 6. Brain and body size estimates in fossil carnivores (after Jerison 1973).

		Brain weight (E) g	Body weight (P) kg	EQ $\left(\frac{E}{kP^{0.66}}\right)$	EQ $\bar{x}$
Creodonts	<i>Thinocyon</i>	5.7	0.80	0.55	0.48
	<i>Cynohyaenodon</i>	8.3	3.0	0.33	
	<i>Pterodon</i>	62	42	0.43	
	<i>Hyaenodon</i>	85	56	0.48	
	<i>Megistotherium</i>	375	354	0.62	
Palaeogene carnivores	<i>Plesictis</i>	11	1.3	0.77	0.61
	<i>Potamotherium</i>	50	9.7	0.92	
	<i>Daphoenus</i> 1	49	26	0.46	
	" 2	66	30	0.54	
	<i>Hesperocyon</i>	15	2.0	0.79	
	<i>Pachycynodon</i>	39	9	0.75	
	<i>Hoplophoneus</i> 1	47	20	0.53	
	" 2	52	49	0.32	
	<i>Eusmilus</i>	38	21	0.42	
	<i>Herpestes</i>	13	2.1	0.66	
	<i>Amphicyon</i>	110	49	0.64	
Neogene carnivores	<i>Plesiogulo</i>	140	38	1.03	0.76
	<i>Mesocyon</i> 1	52	10	0.93	
	" 2	37	9.5	0.69	
	<i>Cynodesmus</i>	36	13	0.54	
	<i>Tomarctus</i>	58	15	0.80	
	<i>Pseudachyurus</i>	89	43	0.60	

be determined with accuracy, and a good deal of inspired guesswork has gone into the estimates. Nevertheless, the figures are reasonably consistent. Taking living carnivores as having an EQ of 1.10, then the mean ($\bar{x}$) for Neogene carnivores is 0.76, that for Palaeogene carnivores 0.61, and that for creodonts is 0.48; that for the marsupial *Didelphis* on this basis is 0.22. That creodonts are about half as intelligent as living carnivores might be a deduction, but the samples are very small and there is considerable overlap in brain size of carnivore families, which is masked by the grouping. When carnivorous mammals are compared with their herbivorous contemporaries, they are seen to be ahead through the Tertiary (Table 7), though the ungulates appear to be steadily narrowing the gap. Radinsky (1975) used a

modified EQ relating brain size to the area of the foramen magnum (Table 8). The foramen magnum area is related to body weight (correlation coefficient 0.65) and is a more readily available parameter. Using brain size-foramen magnum area relationships, Radinsky found that the modified EQ (EQA) was higher for carnivores than for mammals in general. While the families have considerable overlap in range, the mean for canids is higher than that for viverrids, and the latter is higher than that for felids.

TABLE 7. Evolution of relative brain size (after Jerison 1973). Means with sample size in brackets.

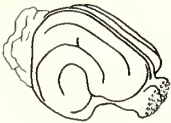
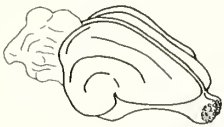
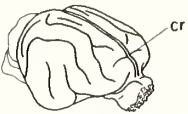
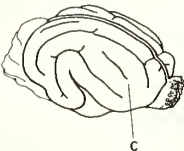
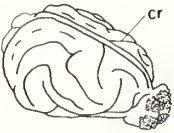
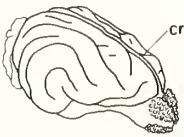
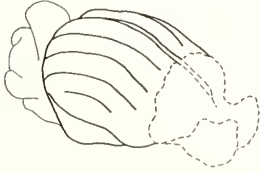
	Ungulates	Carnivores	
Archaic	0.18 (13)	0.48 (5)	Creodonta
Palaeogene	0.38 (26)	0.61 (11)	Carnivora
Neogene	0.63 (13)	0.76 (6)	„
Recent	0.95 (25)	1.10 (15)	„

TABLE 8. Relation of brain size (E) to foramen magnum area (A) (after Radinsky 1975).
(EQA = E/E^a where $E^a = 1.35A^{1.48}$).

	Range	Mean (x)
Canids	1.32-1.70	1.51
Viverrids	0.93-1.58	1.23
Felids	0.98-1.51	1.15
164 species from 5 orders		1.0

A totally different approach to brain studies is that of mapping the cortical areas and tracing the evolutionary changes in the fissure patterns (Radinsky 1968, 1969, 1971, 1973, 1975). Experimental work on living mammals (e.g. Welker and Campos 1963; Welker *et al.* 1964) has shown that the sulci delimit functional areas of the cortex, and to an increasing extent these are becoming identifiable. Radinsky (1968) examined the brain morphology of living otter genera and noted that the coronal gyrus and lateral part of the posterior sigmoid gyrus were usually enlarged. It has been shown that the latter is associated with sensory receptors for the fore limb, while the coronal gyrus is associated with tactile sensitivity in the head region. For otters in water, the efficiency of sight is reduced and that of smell is totally lost; in compensation, otters have increased tactile sensitivity through well-developed vibrissae. The clawless otters feeding on crustaceans and molluscs use their sensitive digits to locate prey. The earliest known lutrine *Potamotherium* has an enormous coronal gyrus, and the bone around the upper lip is densely pitted, strongly suggesting well-developed vibrissae (Savage 1957).

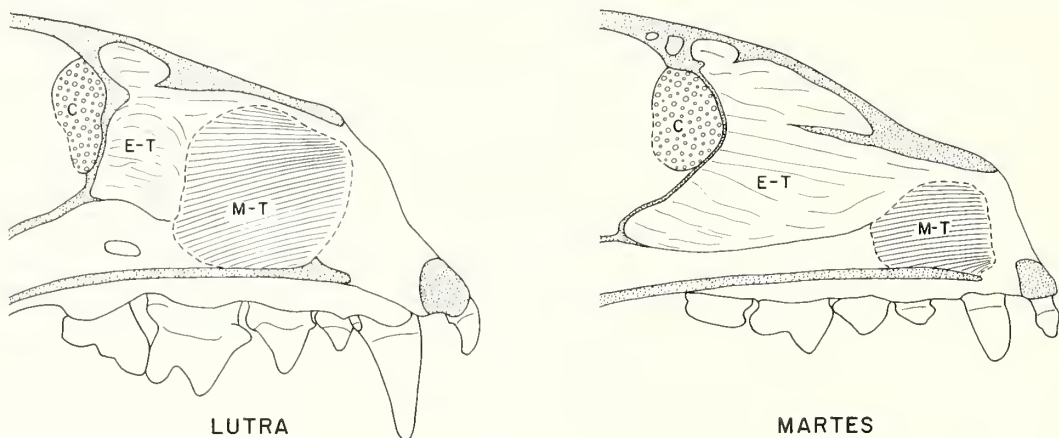
In the evolution of living families of carnivores, Radinsky (1971) has shown that one structure, the cruciate sulcus, has evolved independently at least five times (text-fig. 8); no specific function is yet known for this feature. The brains of living canids are all very similar, except for the prorean gyrus, and canids share with amphyconids some fissure patterns which suggest a relatively close relationship.

	OLIGOCENE	MIOCENE	RECENT
Felidae	 L	 M	 N
Viverridae		 J	 K
Mustelidae	 G	 H	 I
Canidae	 D	 E	 F
	 A	 B	 C

TEXT-FIG. 8. Endocasts of carnivore brains. A, *Daphoenus*. B, *Megistotherium*. C, *Thylacinus*. D, *Hesperocyon*. E, *Mesocyon*. F, *Vulpes*. G, *Potamotherium*. H, *Promartes*. I, *Martes*. J, *Herpestides*. K, *Ichneumia*. L, *Eusmilus*. M, *Proailurus*. N, *Felis*. (B, C, and G original; others after Radinsky 1971). c, coronal gyrus; cr, cruciate sulcus.

With improved techniques of taking endocranial casts, more information is becoming available. Unfortunately there are very few creodont brain casts known, but there appears to be a progressive increase in relative size through time. *Megistotherium* has relatively the largest known brain for a creodont. The pattern is also highly complex and the brain has an unusually large cerebellum.

From the brain we now turn to the senses—smell, sight, and hearing. The olfactory sense leaves in fossils two traces, the turbinal bones and the olfactory lobes of the brain. Though we have few complete endocranial casts, the trend in carnivores seems to indicate that the relative size of the olfactory lobes has increased with time. Radinsky (1975) has shown that the ratio of the olfactory lobes to total brain volume in living carnivores is 2.9% for felids, 4.7% for viverrids, and 5.0% for canids. Turbinal bones, if preserved, provide a second line of approach. There are two sets of turbinals in the nasal area. An anterior set, the maxilloturbinals, is innervated by the fifth cranial nerve and is concerned with warming and filtering the air. Behind these is a second set, the ethmoturbinals, which is innervated by the olfactory nerve; the air passes over these, and the olfactory sense is located here. The relative size of the turbinals is significant. If the maxilloturbinals are much larger than the ethmoturbinals, as in otters, then there is reduced sense of olfaction. If the reverse is the case, as in many mustelines, olfaction is a highly important sense (text-fig. 9).

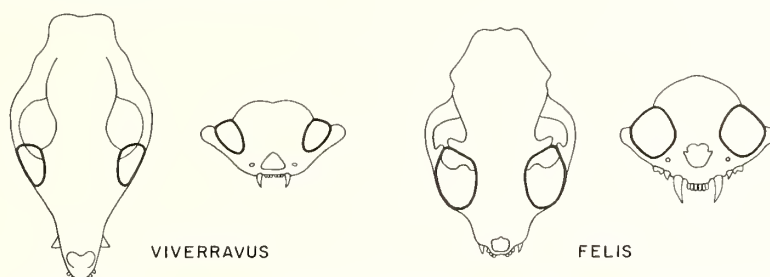


TEXT-FIG. 9. Transverse section of nasal region of two carnivores; to same scale. C, cribriform plate; E-T, ethmoturbinal bones; M-T, maxilloturbinal bones.

Unhappily, few fossil skulls are so preserved that the relative size of the two areas can be determined. In the creodonts *Thinocyon* and *Cynohaenodon* the ethmoturbinals appear to have been relatively large and the animals may, like many mustelids, have hunted mainly by scent. Very reduced olfaction can already be seen in the Early Miocene lutrine *Potamotherium*.

Sight is much more difficult to deduce from the fossil evidence. Firstly, from the orbital area of the skull we can learn nothing of the structure of the eyeball, and hence nothing concerning resolution, distance, diurnal, nocturnal, or colour vision. Further, as much of the information is processed in the eye, the visual areas on the cerebral cortex do not enlarge or increase in complexity in proportion to visual

acuity. But the size of the orbit does provide some clue, and the orientation of the orbits allows us to assess the degree of stereoscopy. Quantitative evaluation of these characters is difficult, but generally in borhyaenids, creodonts, and miacids the eye is proportionately much smaller than in living carnivores. The degree to which the visual fields overlap provides some measure of stereoscopy (text-fig. 10 and Table 9). *Borhyaena* appears to have had the best stereovision among marsupial carnivores; the eyes of *Thylacosmilus* were very small and set facing laterally. Among creodonts, *Patriofelis* had the most forwardly directed eyes, though not as advanced as in living canids, hyaenids, and felids.



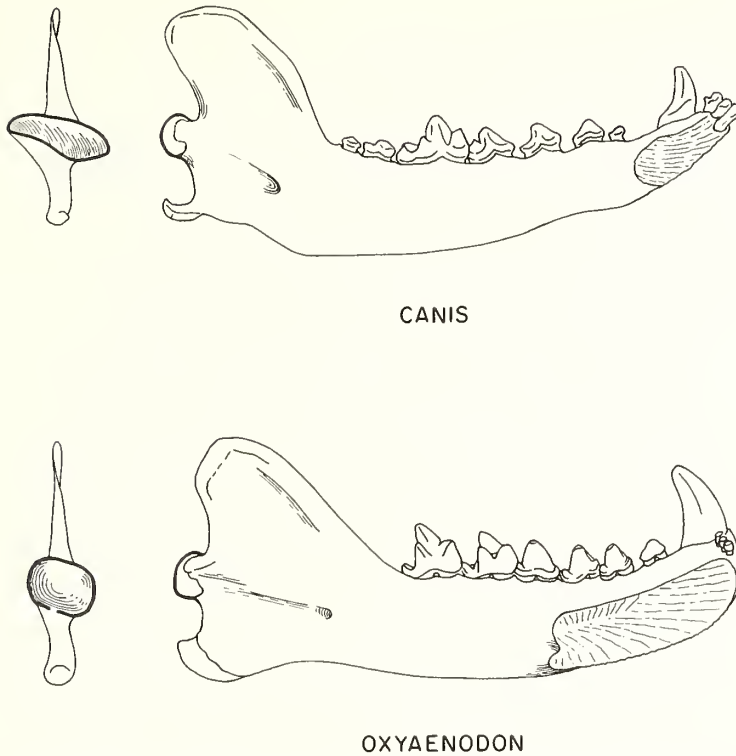
TEXT-FIG. 10. Dorsal and anterior views of miacid *Viverravus* and felid *Felis* skulls to illustrate size and orientation of the orbits (in heavy line).

TABLE 9. Degree of stereoscopic vision in carnivores.

	Marsupialia	Creodonta	Carnivora
Low 30°–50°	<i>Cladosictis</i> <i>Prothylacimus</i> <i>Thylacosmilus</i>	Hyaenodontidae	Miacidae
Medium 50°–70°	<i>Borhyaena</i>	<i>Oxyaena</i> <i>Palaenictis</i>	Amphicyonidae
High 70°–80°		<i>Patriofelis</i>	Ursidae Viverridae Mustelidae
Very high 80°–120°			Canidae Hyaenidae Felidae

The auditory sense is both the most important and the least satisfying sense to study. A great deal of information is often preserved, in both the middle- and inner-ear regions; these are frequently described in great detail (e.g. Hough 1948), yet extremely little of functional significance can be deduced. Hearing is certainly important in most carnivores, and in canids in particular—the bat-eared fox and desert foxes have remarkably large ears and their auditory perception is very acute.

The basic taxonomic divisions within the carnivores are based as much on ear structure as on dentitions. For example, the tympanic bulla is never present on any creodont or miacid. An ossified bulla without a true septum demarcates the canoid and musteloid families, and a bulla with a septum distinguishes the viverroid and feloid families. Recently Hunt (1974) has made a detailed study of the auditory bulla in the context of carnivore evolution.

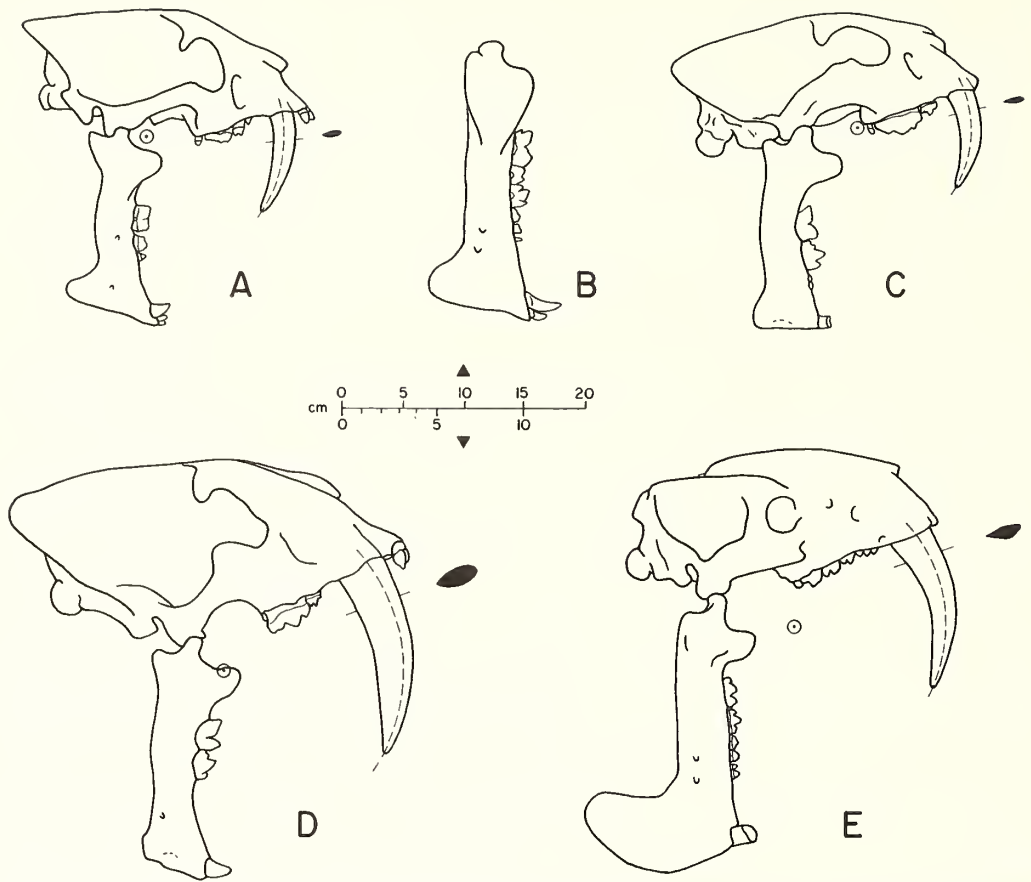


TEXT-FIG. 12. Posterior and internal views of left mandible of creodont *Oxyaenodon* and of canid *Canis*, to illustrate shape and position of condyle and symphyseal area.

condylar joint allows for a shorter and looser symphysis and a lateral slide to bring the carnassials into occlusion. In both lineages the temporal is the main muscle closing the jaw, whereas in ungulates it is the masseter (Smith and Savage 1959). The temporal is well aligned to provide fast action and derives strength from its massive size.

Incisors and canines. The incisors are never specialized in carnivores and usually all three are present; the upper incisors are reduced in number in some short-faced forms and in those with sabre-like canines.

Canines are always present and usually equally well developed in both upper and lower jaws; they are used for biting, piercing, and holding prey. In some lineages they become massive, that is thick in proportion to their length, as, for example, in amphicyonids, ursids, borophagine canids, and some creodonts such as *Megistotherium*. It is, however, the evolution of sabre-like canines that provides the really startling innovations. These have evolved independently in the marsupials with *Thylacosmilus*, in the creodonts with *Apataelurus*, and several times among the felids (text-fig. 13). Associated with the evolution of sabre teeth are changes in the architecture of the skull and mandible, in the musculature for opening and closing

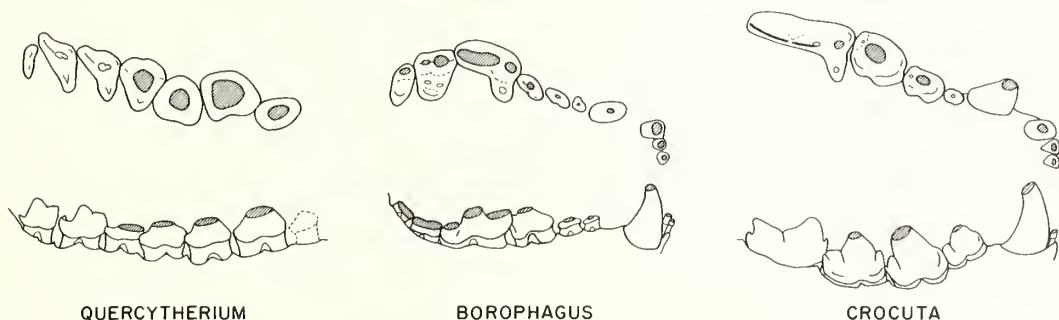


TEXT-FIG. 13. Skulls and mandibles of sabre-toothed carnivores, showing the arcs and centres of curvature of the canines. Transverse sections of the canines in black. A, *Hoplophoneus*. B, *Apataehurus*. C, *Nimravus*. D, *Smilodon*. E, *Thylacosmilus*. (A, C, and D after Matthew 1910, B after Denison 1938, and E after Riggs 1934).

the jaws, and in the musculature for bringing the head down in a powerful sweep to provide the stabbing action. The face is always short; the nuchal crests rise high above and sweep back beyond the occipital condyles. The condyles are often elevated high above the level of the dentition and there is a massive mastoidal area for the attachment of musculature to pull the head downward. The mandibles are slender with weak coronoid processes and are capable of opening wide to give a gape sufficient to clear the line of action of the sabre canines. A bony flange often develops on the ramus to protect the upper canine when the jaws are closed. In transverse section the sabres are usually ovoid, with the posterior edge more acute. While a circular section would be strongest, it would also offer great resistance to penetration; likewise a very thin tooth which would penetrate easily would be liable to damage. Serrations often develop, especially on the more proximal edges of the blade. Riggs

(1934), describing *Thylacosmilus*, stated that the sabre canines were open rooted and continually growing; their roots extend much further back into the skull than in any other sabre-toothed carnivore. The immediate ancestors of the Pliocene *Thylacosmilus* are unknown, although in all features other than the canines it is a normal borhyaenid. The creodont *Apataelurus* is known only from the mandible and is placed with other less fully sabre-toothed taxa in the subfamily Machaeroidinae of the family Hyaenodontidae. Within the Felidae, lineages are not clear; the Oligocene *Hoplophoneus* does not appear to be ancestral to the Plio-Pleistocene machaerodontines, and so sabre-like canines have evolved at least twice within the felids. The absence of any living sabre-tooth forms makes it impossible to be totally certain of their mode of functioning. Simpson (1941) has very fully analysed the mechanics of sabre-like canines, and only the briefest outline need be given here. He detailed the four theoretical ways in which the sabres could function as stabbing weapons to pierce thick skin and sink deep into the flesh, causing the victim to bleed to death; this he considered the principal function of the teeth. Secondarily they may have acted to slice open the carcass, but neither the outline of the teeth and their leading edges, nor the orientation of the musculature of the head and neck are optimally adapted for this, and slicing without prior stabbing would be virtually impossible.

Premolars. In carnivores, premolars have tended with some notable exceptions to remain unspecialized; they are often reduced in number and the anterior ones are lost. The two striking specializations are the development of P⁴ as a carnassial tooth in the Carnivora (these are considered below with molars) and the development of very heavy premolars as crushing teeth, seen in hyaenids, borophagines, and some marsupials and creodonts. In stocks with massive premolars, the teeth become enlarged in girth, remain fairly low crowned and develop thick enamel; usually one or two upper and lower teeth, immediately anterior to the carnassials, are thus modified. It could be argued that, since great power is required to crush bone, these teeth are best situated as far back as possible. But the further back they are, the smaller the gape, and the animals also need to retain a carnassial dentition. The hyaenodont *Megistotherium* had hyaenoid premolars, presumably for bone crushing. In the creodont *Quercytherium* the crushing specialization extends over four teeth (P¹-P⁴) (text-fig. 14). Among the borhyaenids, the genus *Angelocabrerus*

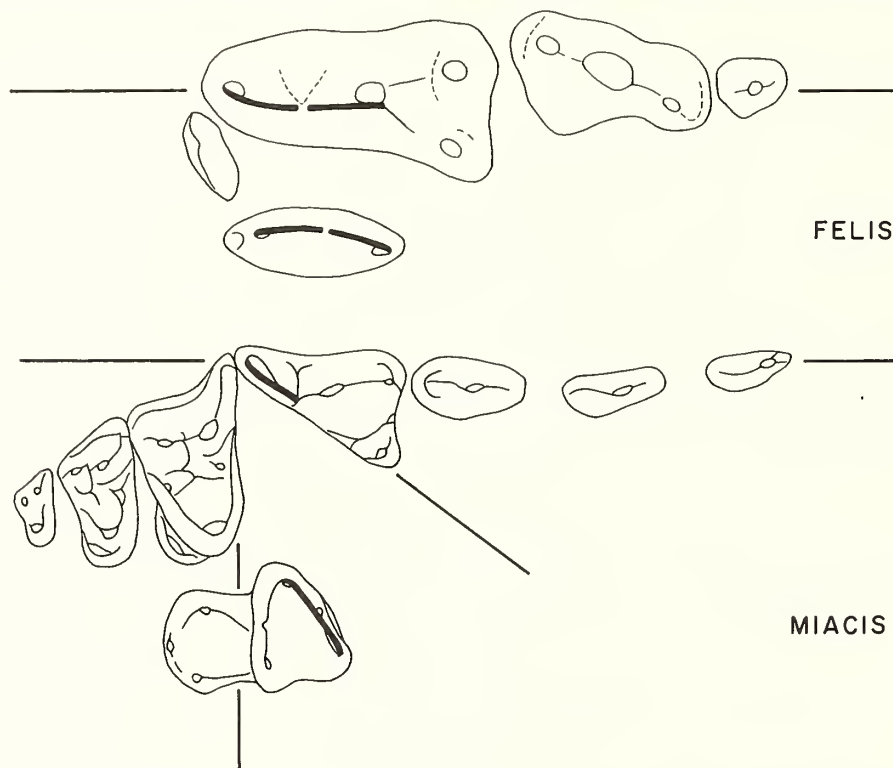


TEXT-FIG. 14. Occlusal views of upper dentitions and lateral views of lower dentitions to illustrate specialized premolars in creodont *Quercytherium*, canid *Borophagus* and hyaenid *Crocuta*. Not to scale.

has a massive P_3 and can be regarded as a likely hyaenoid type. The canid subfamily Borophaginae comprises a suite of large hyaenid-like dogs with heavy crushing premolars in the Neogene of North America.

Molars. The main trends which can be distinguished in the evolution of carnivore molars are the simplification of the tooth pattern, the loss of crushing function in the more truly carnivorous types, the loss of the post-carnassial teeth and the increasing efficiency in carnassialization. The most sophisticated carnassials seen in felids are structurally very simple teeth, and it is in no small part due to this simplicity that the carnassial dentition at its most refined is so successful. This is seen most clearly when one looks at the cheek dentition of a primitive miacid and of a living felid (text-figs. 1 and 15).

In insectivorous stocks, shearing and crushing are performed by two parts of the same tooth. On an upper molar, for example, the metacone provides the blade and the protocone the crushing mechanism, while on the lower molar the paraconid-protoconid becomes the blade and the talonid the basin. This arrangement persists in early creodonts, with the blades enlarged at the expense of the crushing function (text-fig. 16). In the Carnivora, however, since the carnassials are only one pair of



TEXT-FIG. 15. Occlusal view of carnassial dentition in a miacid (*Miacis*) and a felid (*Felis*). Carnassial blades in heavy line. *Miacis* has a diagonal blade and transverse guiding ridge formed by post-carnassial structures; *Felis* has a longitudinal blade and lacks any guiding ridge. Not to scale.

MIACIS



FELIS



HYAENODON



HYAENA



THINOCYON



VIVERRA



SINOPA



MUSTELA



PATRIOFELIS



AILURUS



OXYAENA



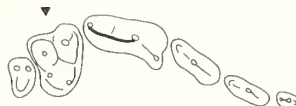
URSUS



THYLACINUS



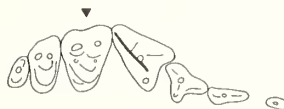
CANIS



BORHYAENA



DAPHOENUS



TEXT-FIG. 16. Occlusal views of upper cheek dentitions of carnivorous mammals. Carnassial blades in heavy line; M¹ indicated with black triangle.

teeth, the more posterior teeth can take on a crushing function for the smaller pieces of food already cut up by the carnassials. Amphicyonids, canids, mustelids, and, to a lesser extent, viverrids exemplify this trend. Ursids and procyonids have secondarily lost the carnassial function and acquired frugivorous, herbivorous, or omnivorous diets, while the insectivorous hyaenid *Proteles* has only a vestigial dentition. In those stocks that have become more purely carnivorous, such as felids and hyaenids, there is a tendency to lose the post-carnassial teeth, with the result that the shearing blades become more posteriorly placed and so a more powerful bite is achieved.

The study of carnassial specialization involves an analysis of the number of teeth involved, the homology of the teeth, their replacement, the posterior migration, the increase in blade size, the angle of shear, the reduction of the non-shearing parts of the teeth, and the self-sharpening devices. The number of carnassials ranges from three pairs (M^1-M^3/M_2-M_4) in many marsupials, through two pairs (M^1-M^2/M_3-M_4) in many creodonts, to one pair (P^4/M_1) in all Carnivora. Usually, when there are several pairs, the carnassial action is not evenly distributed and one pair tends to be dominant, often the more posterior pair. In Carnivora, carnassial shearing is developed in the milk dentition on dp^3/dp_4 . Similarly, in creodonts in which a milk dentition is known, carnassial shearing is developed on the pair of teeth anterior to the permanent successors, usually dp^4/M_1 . In creodonts M_1 is invariably heavily worn, indicating eruption much earlier than the other molars.

THE FORM AND FUNCTION OF CARNASSIAL TEETH

In all early carnivorous mammals, the shearing blades are orientated obliquely across the jaw; in the more truly carnivorous lineages the blade tends to become longitudinal, aligned parallel to the dental row (text-figs. 15 and 16). Functionally a longitudinal shear is easier to operate with food held against the side of the jaws, but the price paid is a loss of total shear length (the diagonal being equivalent to the hypotenuse of a right-angled triangle). However, by becoming longitudinal, there is no longer a need for the transverse guide lines provided by the protocone-paracone in the upper teeth and the protoconid-metaconid in the lower teeth. Hence the protocone and metaconid can become reduced or lost, so simplifying the teeth (text-fig. 1). As the protocone is reduced, so the talonid function diminishes and it too becomes vestigial or lost. All this allows the protoconid-paraconid blade of the lower molar to extend backwards and make up for the loss of length due to the realignment in a sagittal plane. This sequence of trends evolved independently in the oxyaenids, leading to *Palaeonictis* as the most felid-like form, and in the hyaenodontids with *Hyaenodon*. The Carnivora, having only one pair of carnassials, were able to acquire a very large set of shearing teeth and this probably functions better than two pairs, even allowing for replacement, though there is no obvious proof of this.

The length of the carnassial blade is proportional to a the size of the individual, b the size of food chunk that can be swallowed, and c the degree to which the diet is carnivorous.

Another interesting feature of carnassial blades is their shape; they are concave in a vertical plane and plano-convex in a horizontal plane (text-fig. 1). On closing,

the ends of the blades meet first, and only when almost fully closed do the centres meet. The double guillotine action produced by the concave edges allows the maximum force to be exerted on a very small area at a time, and so increases the efficiency of the blade. The concave arc also ensures that the food is trapped between the blades and does not slide out. The terminal pillars of the blades are massive, and the blade thickness tapers towards the centre, where a slit separates the two halves. Opposite the slit the teeth are deeply excavated on the outer face of the P^4 and on the inner face of M_1 ; this creates space for the food during slicing and, by its semi-conical shape, helps to retain the chunk of food in position during cutting. A slit in this area is more efficient than a very thin band of enamel, which would be easily damaged.

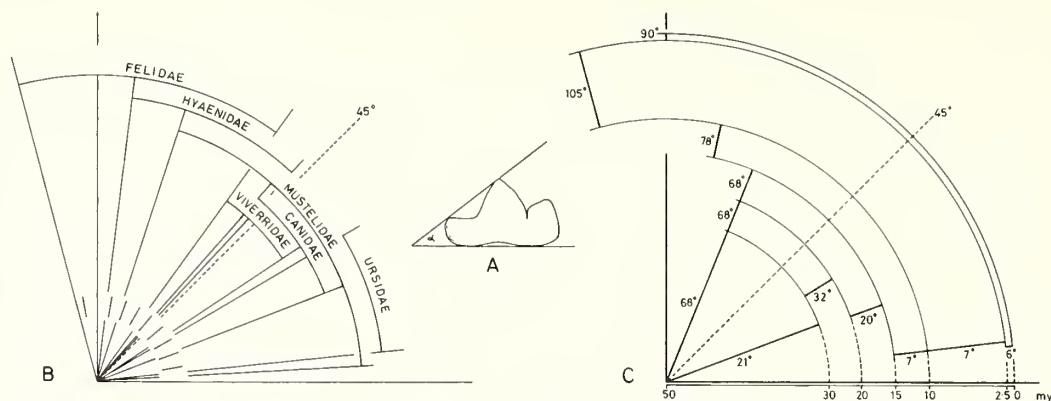
The blade of M_1 is always convex outwards in a horizontal plane; the blade of P^4 is either slightly convex inwards or flat in the same plane. Thus on closing the jaws (text-fig. 1D), contact is made between the two blades at two centrally moving points throughout the traverse. The movement is primarily orthal with a slight medial movement; to allow this, the cylindrical glenoid permits the mandible to slide inwards as it closes, and differential stresses are absorbed in the non-fused symphysis.

Several authors have attempted a quantitative assessment of carnassiality, most recognizing that the trend involves a migration of the shear plane from the diagonal to the longitudinal position. Denison (1938) gave figures for the 'shear angle' (unidentified but presumed to refer to the angle formed by the plane of the paraconid–protoconid shear with the jaw axis). Only three genera were used: *Oxyaena* spp. 60° – 30° , *Protopsalis* very low, and *Patriofelis* 0° , i.e. parallel to the jaw. Butler (1946) measured the anterior and posterior (i.e. lateral) borders of the upper carnassial teeth and gave the maximum value of the ratio of posterior edge/anterior edge; this ratio he divided by the number of carnassial teeth to produce his index of carnassial differentiation. His table comprised nine genera of creodonts, ranging from 0.50 in the primitive genus *Sinopa* to 0.90 in the advanced *Patriofelis*.

Crusafont and Truyols (1956) have given an excellent and original account of carnassiality in carnivores, restricting themselves, however, to members of living families of carnivores and omitting creodonts and miacids. The analysis is based on the measurement of the angle of the blade of the upper and lower carnassial teeth for six families throughout the Cainozoic. For example, the angle formed by the protocone–metastyle–paracone is analysed with the following results: Ursidae 26° – 52° , Canidae 15° – 36° , Mustelidae 19° – 44° , Viverridae 18° – 25° , Hyaenidae 14° – 22° , and Felidae 10° – 25° . The smaller the angle, the more reduced the protocone and the more longitudinal the shear on the metastyle. Ursids are seen to be hypocarnivores, felids and hyaenids hypercarnivores, with viverrids, canids, and mustelids occupying a central position. Similar results are obtained for the lower carnassials. The range of angles is seen to increase with time; in the lower carnassial it is 47° in Eocene–Oligocene and 98° in the Late Miocene–Pliocene (text-fig. 17).

The obvious extension would be to apply the Crusafont and Truyols techniques to marsupials and creodonts. However, frequent lack of good reference points made this difficult, and it was found impossible to achieve consistent and reliable results.

Of prime importance for efficient functioning of the carnassial dentition is the



TEXT-FIG. 17. Range of variation of the carnassial angle in M_1 of living families of carnivores. A, measurement of angle α . B, family range of angle α . C, range of angle α through time (after Crusafont and Truyols 1956).

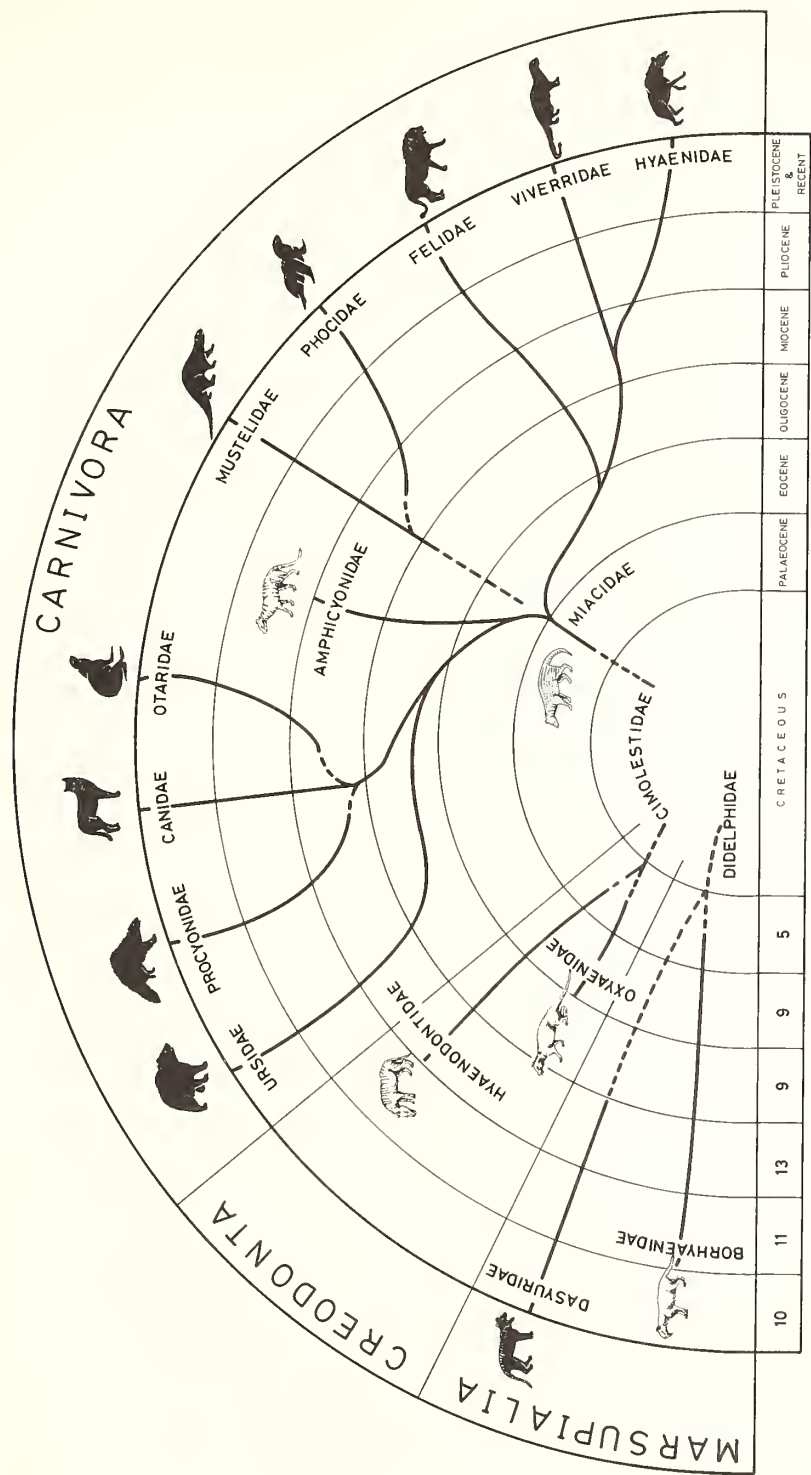
maintenance of a sharp cutting edge, and there are various ways in which this could be achieved. In rodents the incisors maintain a cutting edge by having enamel restricted to one edge so that the softer dentine wears down more rapidly and leaves a sharp edge; this rapid wear is compensated for by continual growth from open roots. In sabre-like canines a serrated edge of enamel is developed, since there is nothing for the tooth to be sharpened against. Neither of these solutions would be efficient in a carnassial dentition. The alignment of the blades is very precise, and the rodent incisor method is unlikely to be adequate. The apposition of two teeth rules out the serrated-edge method, which works only in isolation. This leaves only a self-sharpening device, a process named 'thegosis' by Every (Every and Kühne 1971). The self-sharpening works well on all save a few specialized hyaenodonts which, according to Dr. J. S. Mellett (pers. comm.), continue to enlarge their skulls throughout life and so alter the spatial relationships of the teeth, which turn inward and wear down to the roots in an attempt to counter the effects of size increase.

BIOGEOGRAPHY

The marsupials evolved two successful carnivore lineages. The borhyaenids were the only mammalian carnivores in South America from Palaeocene to Pliocene times; twenty-five genera are known and they range from small otter-like forms to true highly specialized sabre-toothed taxa. Most are poorly known; some reached the size of bears, but none appears to have been truly cursorial. They were only ousted in the Plio-Pleistocene by the invasion of placental carnivores from North America; of these the canids, mustelids, and procyonids have been particularly successful.

The dasyurid marsupials in Australia are less well known in the fossil record, with only two truly carnivorous genera in recent times, of which the thylacine closely paralleled *Canis*.

The creodonts successfully occupied the Palaeogene carnivore niches; they did not survive beyond the Oligocene in North America, but continued on into the



TEXT-FIG. 18. Phylogeny of the carnivorous mammals.

early Miocene in Europe and into the late Miocene in Africa and Asia. The oxyaenids were particularly successful in the North American Eocene with seven genera, all relatively short legged, but with carnassial specializations near to those of felids (e.g. *Patriofelis*). The hyaenodonts were more diverse, with long- and short-faced taxa, with a sabre-toothed group, canid-, felid- and hyaenid-like forms. Some of the latter reached the size of very large bears.

The reasons for the replacement of the creodonts by true carnivores are far from clear. Both groups originated in the Palaeocene, and the creodonts rapidly achieved a dominance in the carnivore niches. The specialized creodonts display many of the characters usually associated with the Carnivora—some had digitigrade feet, some had good stereoscopic vision, some had highly efficient carnassial dentitions, and yet others had large and complex brains. The history of replacement is paralleled in those of the replacement of the multituberculates by the rodents, the perissodactyls by the artiodactyls, and the archaic ungulates by the modernized ungulates. The most recent example is that of the replacement in Australia of the thylacine by the dingo. No one single factor can be cited to explain the change; in an intensely competitive field the combination of slight advantages are favoured by natural selection; only a thorough field study of the ecology and behaviour of each stock would enable these to be quantified. In the early stages of evolution, the advantages appear to have lain with the creodonts, and only after 20 million years did the balance tip in favour of the Carnivora. None the less, the Carnivora have been about four times as successful as the creodonts; creodonts are known from 45 genera spanning about 45 million years, while Carnivora, excluding living and aquatic genera, are known from 218 genera over a span of about 55 million years.

The fossil record of early Palaeogene Carnivora is poor, but by late Eocene times nearly all the terrestrial carnivore families had become established in Holarctic realms. The amphicyonids occupied canid, ursid, and hyaenid niches, to be replaced later by stocks of these modern families. The canids are the most ubiquitous of carnivores, found on all continents save Antarctica. They are usually medium sized and never achieve the degree of specialization found in felids and hyaenids, which may in part account for their success. The mustelids, occupying Holarctic realms, and the viverrids, occupying tropical realms, dominate the smaller-sized carnivore stocks, exploiting the vast potential of rodent prey, though usually supplementing it with other foods. The hyaenids are the youngest family and occupy ossifagous niches in the Old World. The felids can truly be regarded as the acme of carnivore evolution; though limited today to a few genera, their many species are very widely distributed. In almost all their skeletal elements, in their senses and dental apparatus, they represent the ultimate in carnivore achievement.

CONCLUSIONS

Carnivores comprise about 10% of all mammalian genera and about 2% of the mammalian biomass.

Carnivore specialization is defined as having a carnassial dentition and a substantial proportion of vertebrates in the diet.

Carnivore stocks evolved twice among the marsupials (borhyaenids and dasyurids)

and twice among the placental mammals (Creodonta and Carnivora). Borhyaenids were the only mammalian South American carnivores until the Pliocene, dasyurids filled a similar role in Australia until Recent times. Creodonts were gradually replaced by Carnivora in North America during the Oligocene, and in Africa and Asia during the late Miocene.

The vertebral column of carnivores is strong and flexible, and the tail is usually long. In creodonts the vertebral column was less flexible than in living carnivores.

The limbs of carnivores are multi-purpose organs and do not become highly specialized, though most acquire some cursorial adaptations. They are relatively shorter in the Creodonta than in the Carnivora. Aquatic carnivores always have short limbs, and cursorial forms have long limbs. The foot is usually the shortest element of the three segments of the limb, whilst in herbivores the foot is the longest. Primitive carnivores have plantigrade feet, but advanced creodonts and all cursorial carnivores have fully digitigrade feet.

The brains of creodonts are smaller and simpler than those of living carnivores, but the brains of carnivorous mammals are always relatively larger than those of the contemporary herbivores.

The olfactory sense in creodonts was probably at least as good as in living carnivores. Sight, however, was probably not as good, and fully stereoscopic vision developed only rarely in carnivorous marsupials and creodonts, whereas it is common in canids, hyaenids, and felids. Hearing is acute in canids, felids, and viverrids and is particularly acute in carnivores living in warm arid environments.

The mandibles in most creodonts were loose fitting with long firm symphyses, and the carnassials required transverse guiding ridges to ensure precise occlusion. The mandibles of the Carnivora are tightly fitting with no need for long symphyses and guiding ridges; their carnassial blades have rotated from an oblique angle to a longitudinal position in the most specialized forms (canids, hyaenids, and felids). The most advanced creodonts were more specialized than the primitive Carnivora.

The canine teeth are usually well developed and may become specialized as stabbing sabre-like teeth: this trend evolved independently in three stocks—marsupials, creodonts, and felids.

Premolar teeth in some marsupials, creodonts, and Carnivora have become massively large to function as bone-crushing tools, and in a few cases to act as mollusc-shell crushers.

The principal trend in the evolution of molar teeth is one of simplification, by the reduction or loss of the crushing function and loss of the post-carnassial dentition.

The evolution of the carnassial dentition involves three, two, or one pair of teeth. The most advanced forms have only one pair, which is large and devoted solely to shearing by loss of all other parts of the teeth not concerned with cutting. The cutting edges of the blade are self-sharpening.

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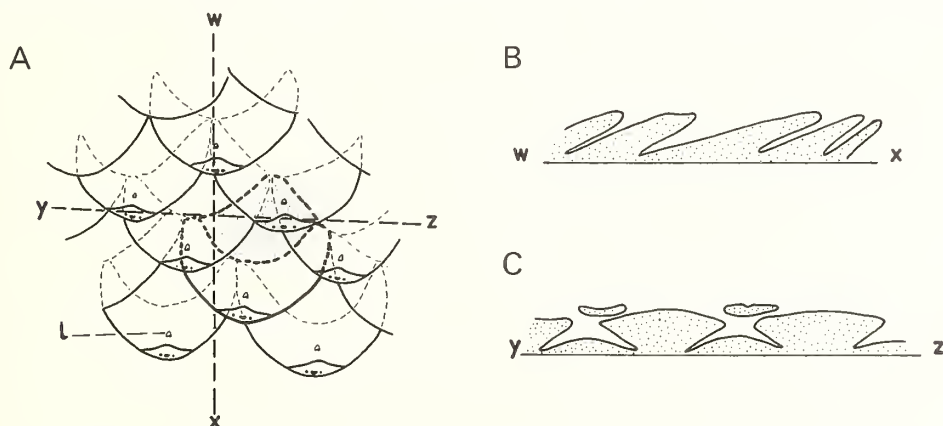
EPIDERMAL STUDIES IN THE INTERPRETATION OF *LEPIDOPHLOIOS* SPECIES

by B. A. THOMAS

ABSTRACT. Epidermal details are described from the leaf cushions of five species of *Lepidophloios* including one new species *L. grangeri*. Such epidermal information allows the species to be distinguished more accurately. Cushion variation within a species is also considered, with epidermal studies verifying the conspecificity of specimens. It is suggested that young *Lepidophloios* cushions are of the *Lepidodendron* form, which subsequently enlarged to increase their photosynthetic ability.

LEPIDOPHLOIOS is a genus of arborescent lycopod stems very similar to *Lepidodendron* in size, general morphology, and in having a dense covering of spirally arranged leaves. All but the terminal shoots of both genera shed the apical parts of their leaves, retaining only their basal portions as the familiar leaf cushions. The main distinguishing feature is that in *Lepidophloios* most cushions characteristically bulge outwards and downwards in such a manner that they overlap each other and show rounded lateral and basal angles (text-fig. 1). The leaf scars appear at the bases of the visible portions of the leaf cushions and are always broader than long, usually with one vascular print and two parichnos scars. Therefore the only part of the cushion normally visible is the upper half representing the basal portion of the adaxial leaf surface. The lower half, or abaxial surface, is hidden.

Confusion has, however, existed about the separation of these two genera and opinions have varied about the determinations of some specimens. This problem



TEXT-FIG. 1. Drawings to illustrate the main feature of the *Lepidophloios* leaf cushion. A, leaf cushions, l—ligule pit aperture. The stippled area of the heavy print cushion represents the area of connection of the cushion to the stem. B and C, diagrammatic sections through uncompressed leaf cushions. The lines of section are shown on fig. A.

is accentuated when specimens are mistakenly inverted. For example, specimens of *L. acerosus* Lindley and Hutton have been mistaken for species of *Lepidodendron* and figured inverted, while specimens of *Lepidodendron* have been figured upside-down and described as species of *Lepidophloios*. Such determinations have naturally proved troublesome in the literature and the more important are returned to later.

Confusion of this kind is best avoided by careful study and recognition of the finer cushion details. General shape with suggestions of cushion overlap is insufficient for generic determination as a few species of *Lepidodendron* show this feature in their upper angles (e.g. *L. mannabachense* Presl., Thomas 1970, pl. 32, figs. 3, 4, 6, 7). One such specimen from the Black Bed Coal of Yorkshire clearly illustrates such a possible confusion. Both Kidston (1893, p. 555, pl. 1, fig. 4) and Crookall (1964, p. 307, pl. 75, fig. 6) described it as *Lepidophloios laricinus* but I believe it to be *Lepidodendron mannabachense*. I have therefore figured some of its leaf cushions correctly and inverted to show how one can be misled by incorrect orientation (Pl. 33, figs. 1, 2). Such cushions presumably bulged outwards more above than below the leaf scars which could then have given this marginal overlap during compression. It is far safer to look for the ligule pit apertures, the parichnos, and the foliar prints, as their positioning is only slightly variable. The ligule pit is always above the leaf scar; the parichnos, when present, are invariably below the leaf scar; while the three foliar prints normally form an arc in the lower half of the leaf scar with the vascular print being slightly below the level of the other two. Even surface ornamentation can sometimes be a valuable guide as certain *Lepidodendron* species have their cushions distinctly striated above the leaf scar which is a feature not shown by *Lepidophloios*.

The cushion cuticles are described here in some detail for the first time, although certain structural details of their guard cells have already been discussed (Thomas 1974). All show the same general arrangements of epidermal cells and stomata as those described from *Lepidodendron* (Thomas 1970). Cuticle was prepared by macerating portions of compression in Schulze solution (concentrated nitric acid and about 5% potassium chlorate) normally followed by clearing in dilute ammonia solution. Some cuticles were mounted unstained in glycerine jelly and examined by normal transmitted light, supplemented in some instances by phase-contrast illumination. These prepared slides have been deposited with their respective specimens. Other cuticles were coated with gold/palladium and studied with a 'Stereo-scan' Scanning Electron Microscope. A range of specimens was examined for most species in an attempt to detect any variation, but this was often prevented by a lack of suitable material. Many specimens are preserved as impressions from which all the compression has either disappeared during fossilization or has been removed since collection. Even when some compression remains it is often badly cracked so that it does not yield cuticle in usable-sized fragments.

The most important specimens examined are listed for each species discussed. They belong to, or were deposited in, the British Museum of Natural History, London (BMNH); the Czechoslovakian National Museum, Prague (CNM); the Institute of Geological Sciences: Kidston Collection, London (K) and the general collections of London (IGSLond), Leeds (IGSLds), and Edinburgh (IGSE).

SYSTEMATIC DESCRIPTIONS

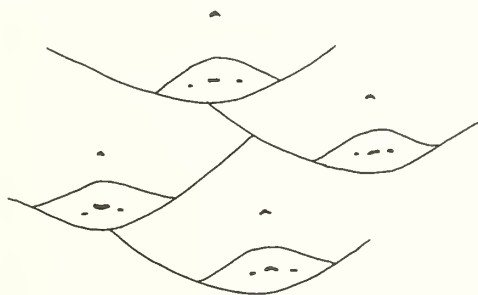
Lepidophloios laricinus Sternberg

Plate 33, figs. 1-6; Plate 34, figs. 1-3; text-figs. 2, 3

- 1820 *Lepidodendron laricinum* Sternberg, p. 21, pl. 11, figs. 2-4.
 1875 *Lepidophloios laricinum* Sternberg; Feismantel, p. 191, pl. 33, figs. 1-4; pl. 34, figs. 1-4.
 1904 *Lepidophloios laricinus* Sternberg; Zalesky, pp. 30, 99, pl. 6, figs. 8, 10; pl. 7, figs. 1, 2; pl. 8, figs. 7, 9.
 1964 *Lepidophloios laricinus* Sternberg; Crookall, pars, p. 307, pl. 74, fig. 5; text-figs. 98, 100c.

Material. Type specimen, CNM ČGH316, from the Wranowitz Shaft in the Radnice Coalfield, Central Bohemia (uppermost Westphalian B-C); BMNH V58739 from Kamenný Újezd, near Nýřany, Plzeň district, West Bohemia (Upper Westphalian B-D?); IGSLds V4486b from above the Main Seam, Newbiggin Colliery, Northumberland—Westphalian B; IGSLond 15027 from Dysart, near Kirkaldy, Fife—Westphalian A or B.

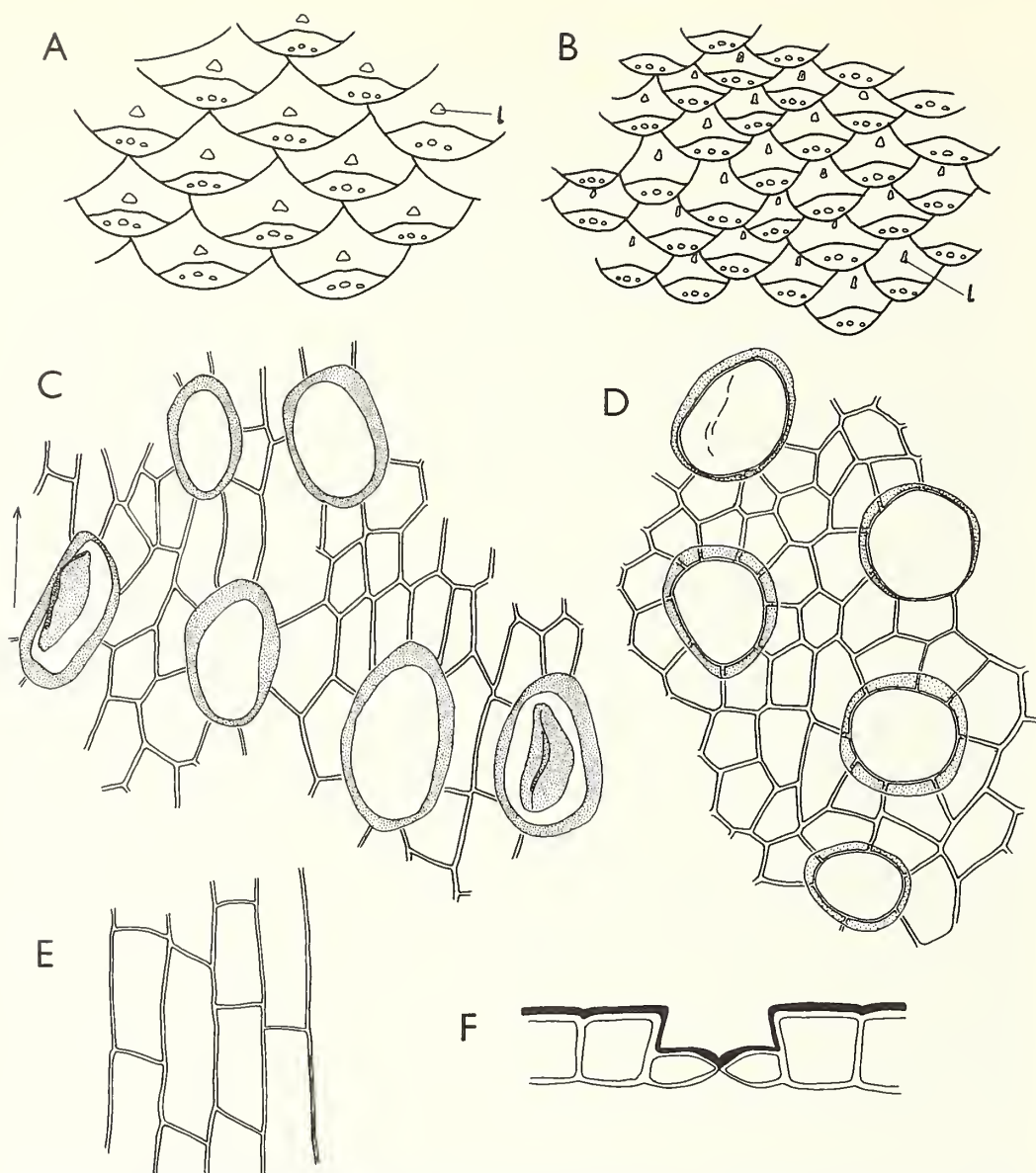
All the specimens accepted here are of the same general cushion morphology in having downward bulging and overlapping leaf cushions. They all appear to be from mature stems, mostly of large diameters, and none are known which might be thought to come from terminal shoots still retaining the distal lamina portions of their leaves. Visible portions of the overlapping cushions are normally much broader than long although in a few specimens these dimensions are nearly equal. Distinct keels are never present on the cushions but sometimes their surfaces bulge in the median line giving the appearance of a very indefinite keel. The three foliar prints are usually in the lower half of the leaf scar but occasionally they can be found in the upper half. The type specimen was figured by Sternberg without ligule pit apertures on the leaf cushions, but re-examination shows indistinct pit scars about 1.5 mm above the leaf scars (text-fig. 2). This species has often been quoted as having its ligule pit scars a little distance above the leaf scars and in general comparison with other species this appears to be correct. Crookall (1964) cites K 6142, from Glenburn and Hilton Colliery, Skelmersdale, Lancashire, as an exception to this. However, as the visible cushion areas are only 2.0 mm long and 3.5 mm broad, one can hardly expect there to be a very large distance between these two scars. Cushion size will naturally determine the length or area of certain individual features and no definite sizes or areas should ever be quoted.



TEXT-FIG. 2. *Lepidophloios laricinus* Sternberg.
Type specimen CNM ČGH316, · 2.

The type specimen is an impression and unfortunately the very little remaining compression gave no cuticle. Preparations were, however, made from BMNH V58739, which came from the same area as the type, and from IGSLds V4486b and IGSLond 5027.

Cuticle description. The epidermal cellular arrangement appears to be virtually identical on both the exposed and hidden leaf cushion surfaces. Most of the cells



TEXT-FIG. 3. *Lepidophloios laricinus* Sternberg. A, BMNH V4486b, $\times 2$. B, IGS Lond 15027, $\times 2$, 1—ligule pit aperture. C–F, cuticle from BMNH V58739. C, cuticle from median area of the cushion, $\times 400$; drawn from the undersurface; slide no. V58739a. Arrow directed parallel to the vertical axis of the cushion. D, cuticle from the non-median area of the cushion, $\times 400$; drawn from the undersurface; slide no. V58739b. E, ligule pit cuticle, $\times 400$; slide no. V58739c. F, diagrammatic median transverse section of a stoma, $\times 500$.

EXPLANATION OF PLATE 33

Figs. 1 and 2. *Lepidodendron mannabachense* Presl. K 1404 from above the Black Bed Coal, Low Moor, Yorkshire; both illuminated from the top left, $\times 3$. 1, orientated correctly. 2, inverted showing '*Lepidophloios*' characters.

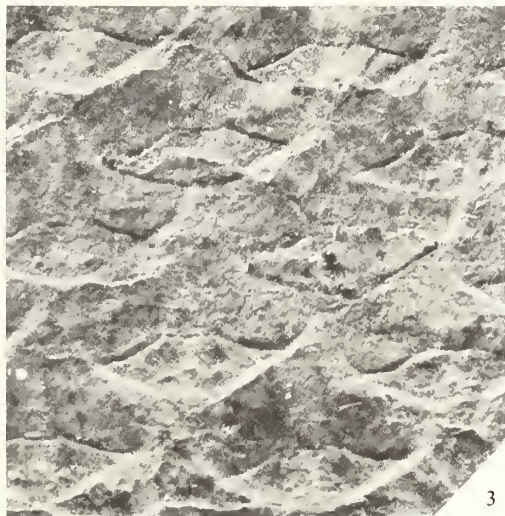
Figs. 3–6. *Lepidophloios laricinus* Sternberg. IGS LDs V4466B from above the Main Seam, Newbiggin Colliery, Northumberland, $\times 4$. 4–6, cuticle prepared from BMNH V58739; 4, SEM., $\times 200$; 5, 6, transmitted light photographs; slide no. V58739a, $\times 350$.



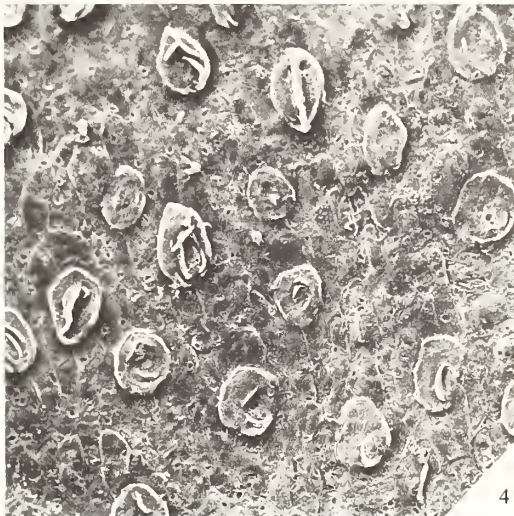
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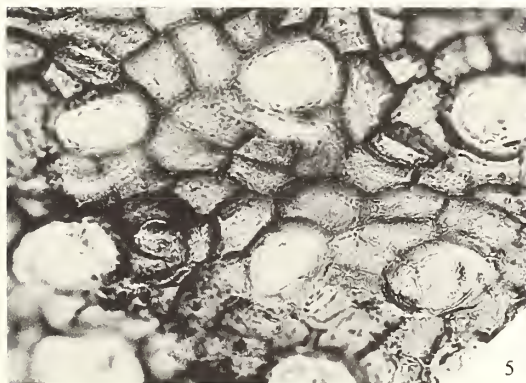
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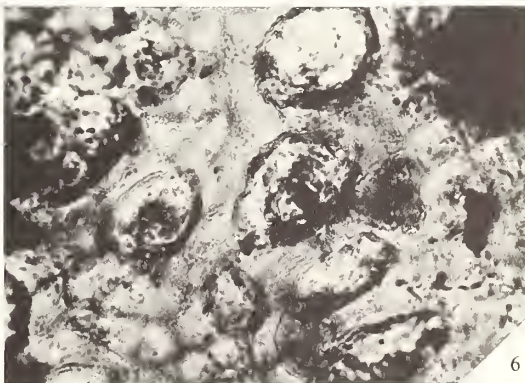
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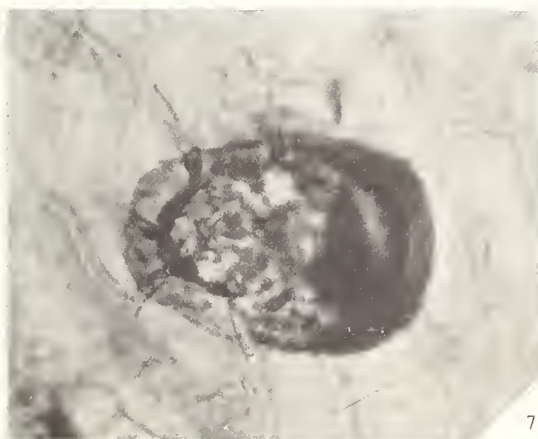
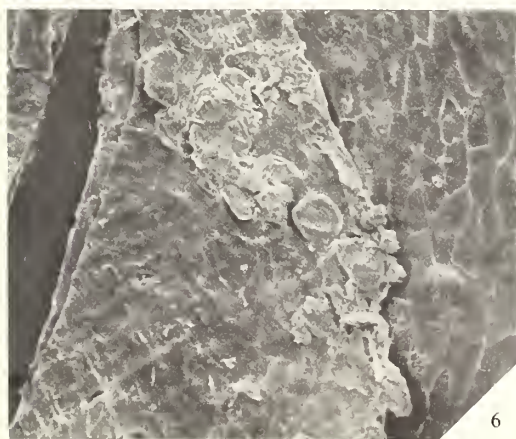
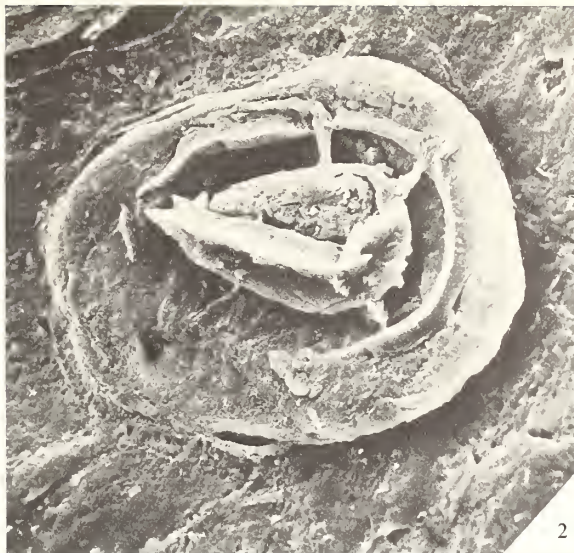
are elongated along the length of the cushion and about $40\text{ }\mu\text{m} \times 15\text{ }\mu\text{m}$ in size, although those near the cushion sides are isodiametric and about $15\text{ }\mu\text{m}$ large. Their anticlinal walls are straight, smooth, and $2\text{ }\mu\text{m}$ thick, while the periclinal walls are flat and smooth. Stomata are randomly arranged on the cushion at about 250 per mm^2 and orientated roughly parallel to the vertical axis of the cushion. Individual stomata have an average size of $45\text{ }\mu\text{m} \times 30\text{ }\mu\text{m}$, having an observed range of about $40\text{--}60\text{ }\mu\text{m} \times 23\text{--}40\text{ }\mu\text{m}$, with guard cells sunken in pits about $6\text{--}10\text{ }\mu\text{m}$ deep. The ligule pit cuticles are about 0.7 mm broad, but no length measurements were possible due to their fragmentation during preparation. The pit wall cells are rectangular, $50\text{ }\mu\text{m} \times 16\text{ }\mu\text{m}$ large, longitudinally elongated, and in vertical rows. The anticlinal walls are straight, smooth, and about $2\text{ }\mu\text{m}$ thick; the periclinal walls are flat and smooth.

Comparison. *L. laricinus* has been described from both the Upper and the Lower Carboniferous rocks of Great Britain, but it is here restricted to the Upper Carboniferous with a reassignment of the Lower Carboniferous specimens. K 1828, from the Carboniferous Limestone Series of Grange, Linlithgowshire in Scotland, was originally described by Kidston (1893*b*, p. 560) as *L. macrolepidotus* and by Crookall (1964) as *L. laricinus*. Here I am redescribing it as *L. grangeri* sp. nov. (p. 286). IGSE 1296, described by Crookall (1939, p. 14, pl. 2, fig. 2) from the Scottish 'Millstone Grit' at Cambus, near Alloa, Clackmannanshire, has already been referred to *Lepidodendron rhodianum* Sternberg (Thomas 1970, p. 168, text-fig. 12). The specimens of *Lepidophloios laricinus* described by Crookall (1964, p. 310) from the Carboniferous Limestone Series of Scotland differ in two aspects of cushion morphology. They have more prominently raised median areas to their cushions and have ligule pit apertures adjacent to the upper edges of the leaf scars. No cuticles could be prepared, but the differences in cushion morphology seem sufficient to strongly question their inclusion within this species and it seems more prudent to keep them separate. They are equally unlike all the other described species, but it is not intended at present to give them a new name. This view is then in agreement with that of Kidston who had originally labelled these specimens as *Lepidophloios* sp.

Those specimens (K 4991–4992) quoted by Crookall (1964, p. 312, pl. 74, figs. 3, 4) as examples of small shoots showing upturned and undeflected leaf cushions are also excluded here from this species. They are instead reassigned to Kidston's original determination of *L. acerosus* on the basis of both cushion morphology and epidermal characters seen in cuticle preparations.

EXPLANATION OF PLATE 34

- Figs. 1–3. *Lepidophloios laricinus* Sternberg. Cuticles prepared from BMNH V58739. 1, cushion cuticle; SEM., $\times 500$. 2, stoma; SEM., $\times 1500$. 3, ligule pit cuticle; slide no. V58739c, $\times 350$.
 Figs. 4–7. *Lepidophloios acerosus* Lindley and Hutton. 4, K 4947 from above the Parkgate Coal (Old Hards), Hartley Bank Colliery, Horbury, Yorkshire, $\times 1$. 5, K 764 from above the Kiltongue Coal, Foxley, near Glasgow, $\times 2$. 6, SEM. showing cushion cuticle from above and below the leaf scar of K 764, $\times 200$. 7, stoma photographed with transmitted light; slide no. PF 3195, $\times 1200$.



Lepidophloios acerosus Lindley and Hutton

Plate 34, figs. 4–7; Plate 35, figs. 1, 2; text-fig. 4

- 1831 *Lepidodendron acerosum* Lindley and Hutton, pl. 7, fig. 1; pl. 8.
 1837 *Lepidostrobus pinaster* Lindley and Hutton, pl. 198.
 1893b *Lepidophloios acerosus* Lindley and Hutton; Kidston, p. 558, pl. 1, fig. 1; pl. 2, fig. 9.
 1901 *Lepidophloios acerosus* Lindley and Hutton; Kidston, p. 54, text-fig. 7c (inverted).
 1914 *Lepidophloios acerosus* Lindley and Hutton; Arber, pp. 396, 415, 444, pl. 28, fig. 20 (inverted).
 1917 *Lepidophloios acerosus* Lindley and Hutton; Kidston, pp. 1057, 1080, 1083, pl. 2, fig. 5 (inverted).
 1929 *Lepidophloios acerosus* Lindley and Hutton; Crookall, p. 26, pl. 3, fig. 50; pl. 22, fig. k (both inverted).
 1974 *Lepidophloios acerosus* Lindley and Hutton; Crookall, p. 313, pl. 75, fig. 7; pl. 76, fig. 2; pl. 79, fig. 5 (inverted); text-fig. 100d.

Material. K 764 from above the Kiltongue Coal, Foxley, near Glasgow, Lanarkshire—communis Zone, Westphalian A; K 3459 from above the Fenton Coal, Dodworth Colliery, near Barnsley, Yorkshire—communis Zone, Westphalian A; IGSLds RC 1778 from above the Ince Yard Mine, Mains Colliery, near Wigan, Lancashire—modiolaris Zone, Westphalian A; K 4991 and BMNH V33591 from above the Barnsley Red, Monkton Main Colliery, near Barnsley, Yorkshire—similis pulchra Zone, Westphalian B; IGSLond KP 449 from above the No. 5 seam Chislet Colliery, Kent—Transition Coal Measures, Westphalian ?C; K 6284 from above the Hafod Rider Seam, Hill's Plymouth Colliery, Pentrebach, near Merthyr, Glamorgan—upper similis pulchra Zone, Westphalian B; K 6142 from Glenburn and Hilton Colliery, 1 mile NE. of Skelmersdale, Lancashire—Westphalian ?; K 3634, from above the Fulledge or Yard Mine, New Shaft, Bank Hall Colliery, Burnley, Lancashire—Westphalian B; K 4992 from above the Pargate Coal, Church Lane Colliery, Dodworth, near Barnsley, Yorkshire—modiolaris Zone, Westphalian A.

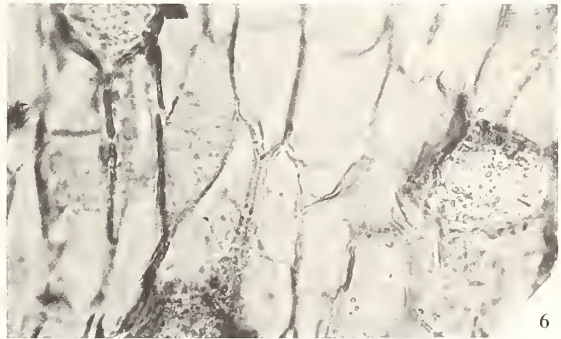
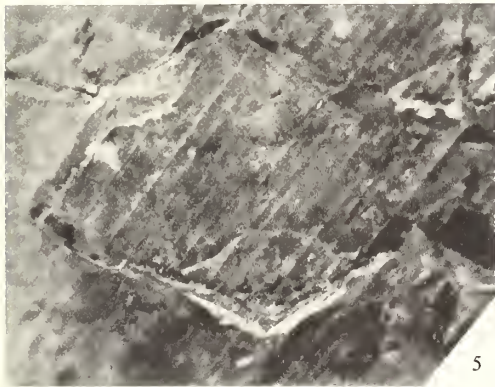
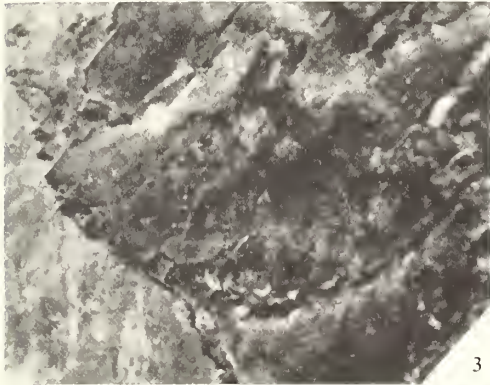
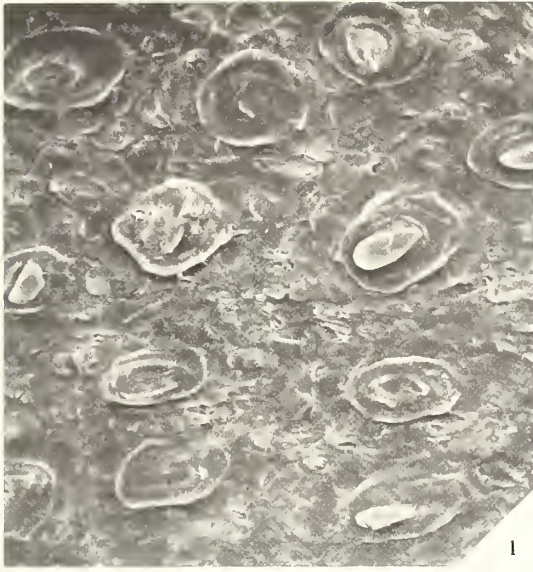
The widely recognized and described form of *L. acerosus* is a typical '*Lepidophloios*' stem with downturned and overlapping leaf cushions. The exposed cushion areas are longer than broad but their relative dimensions vary slightly with size and the amount of interdependent overlap. Definite cushion keels are usually present but in some specimens they are only slightly raised. The three foliar prints are usually in the lower halves of the leaf scars although they are sometimes nearly central. Ligule pit apertures occur just above the leaf scars, although as Crookall (1964, p. 312) has shown they can be sometimes slightly separated.

The smallest shoots are rather different in having undeflected smaller leaf cushions which could be referred to the genus *Lepidodendron*. Specimens K 3634, K 4991–4992, K 6142, and K 6284 possess cushions of this kind, while BMNH V33591 also possesses more 'normal' slightly elongated and downward deflected, leaf cushions as its lower end. Kidston (1893b, pl. 1, fig. 1) described a small leafy shoot with upturned leaf cushions as *Lepidophloios acerosus*, but I would agree with Jongmans

EXPLANATION OF PLATE 35

Figs. 1, 2. *Lepidophloios acerosus* Lindley and Hutton. Cuticle from the cushion surface above the leaf scar of K 764. 1, SEM. photograph showing stomata and epidermal cells, $\times 500$. 2, cushion cuticle with ligule pit cuticle; slide no. PF 3196, $\times 125$.

Figs. 3–6. *Lepidophloios macrolepidotus* Goldenberg, from the roof of the Fenton Coal, Dodworth Colliery, near Barnsley, Yorkshire. 3, K 3256, $\times 3$. 4, K 3257, $\times 3$. 5, 6, cuticle from K 3256; slide no. PF 2895. 5, $\times 250$; 6, $\times 550$.



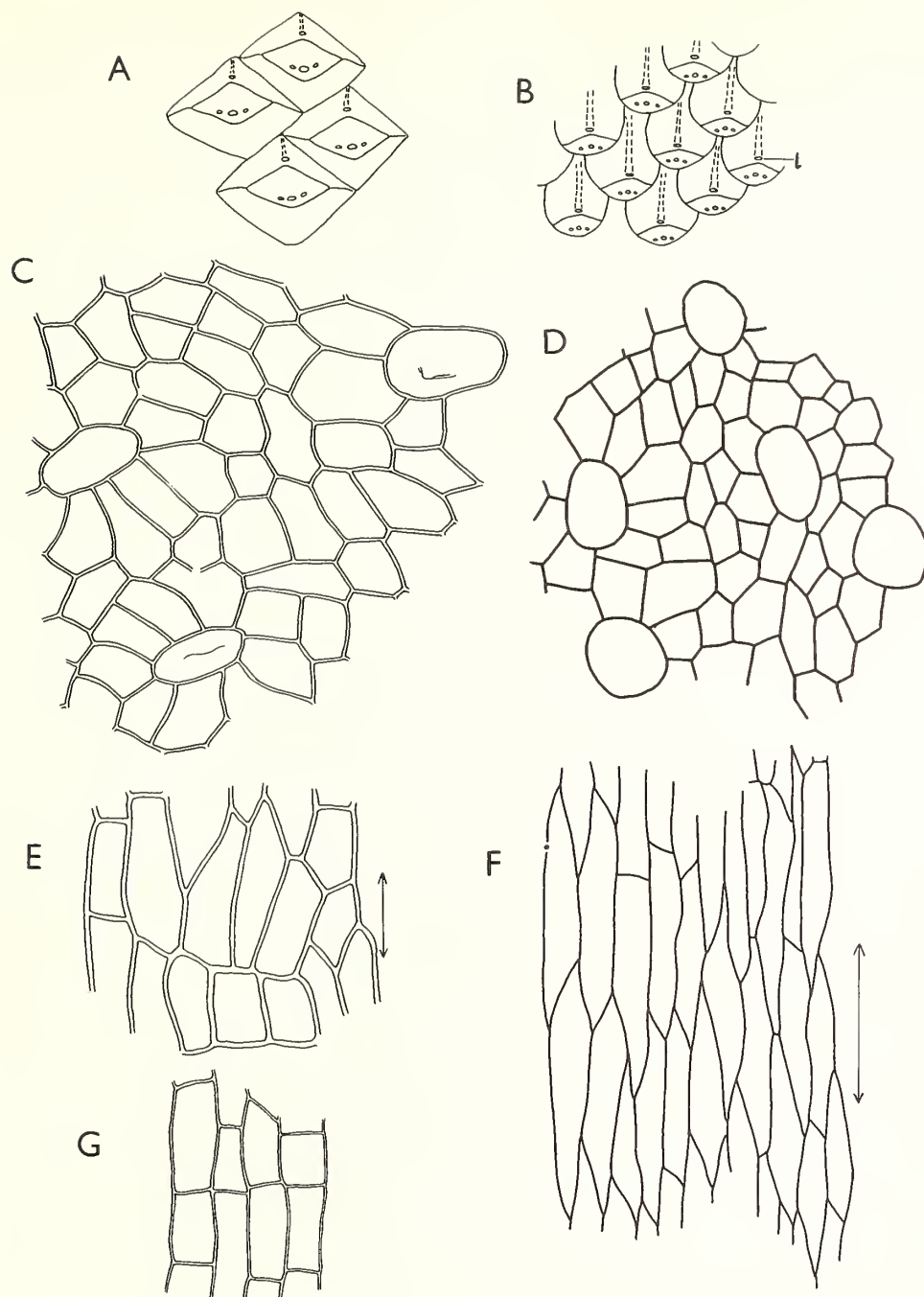
(1930, p. 40) and Crookall (1964, p. 315) that, on the basis of the visible cushion morphology, there appears to be no good reason for including it within this species.

A comparison of these stems reveals several interesting facts which are relevant to a consideration of their growth patterns. The undeflected cushions of K 4991 and K 4992 are about 5.0 mm long and 5.5 mm broad, therefore being larger than the smallest of the 'more usual' deflected cushions of IGSLond 3459. The cushions on K 764 and K 4947 show a progressive increase in size down the stem, while the former also exhibits a corresponding increase in shoot diameter. There are therefore shoots with either non-deflected or deflected leaf cushions suggesting that this may be an expression of subsequent growth of the cushions; an idea supported by those specimens showing a gradual basipetal increase in cushion size. This is clearly a complex subject which is not yet fully understood but we shall return to it in the general discussion.

Cuticle description. Preparations have been made from a selection of specimens with undeflected and deflected cushions and from cushions of varying sizes. Certain general characteristics can be given for the species although certain slight variations have been noticed. The epidermis is different on the two cushion surfaces (Pl. 34, fig. 6). The epidermal cells from the exposed adaxial surface are isodiametric and about 15–20 μm large over most of the central area, but near the sides they are roughly 30 μm $\times$ 15 μm and elongated towards the cushion margin. The cells from the hidden abaxial surface are about 60 μm $\times$ 10 μm large and elongated along the cushion length. Small fragments of cuticle with cells about 50 μm $\times$ 15 μm large were obtained from some of the larger specimens and although their exact origin is unknown it is suggested that they may have come from the intercushion connecting areas of the stem surface. All the cells have straight, smooth anticlinal walls and flat, smooth periclinal walls. Stomata are present almost solely on the exposed cushion surface (about 180 per mm^2) although a few have been noted on the hidden surface—near the edges where the cells are also not quite so elongated. The average stomatal size is about 35 μm $\times$ 26 μm with their guard cells superficial or only very slightly sunken. Details of guard cell anatomy have already been given (Thomas 1974, p. 530) and I can add no more to this at present. The ligule pit cuticles have rectangular cells, 25–30 μm $\times$ 10 μm large, arranged in vertical rows, with straight, smooth anticlinal walls and flat, smooth periclinal walls.

Comparison. The leaf cushions of *L. acerosus* and *L. laricinus* can be distinguished by a number of characters. The cushions of *L. acerosus* are relatively longer and possess definite keels which are never present in the other species. Ligule pit positions are also important as they are normally immediately above and adjacent to the leaf scars in *L. acerosus* but a short distance above them in *L. laricinus*. The cuticle preparations support the distinction between the two species as the epidermal arrangement is different above and below the leaf scars in *L. acerosus* but in *L. laricinus* there is no such distinction. Also the guard cells are sunken in deep pits in *L. laricinus* while they are superficial or only very slightly sunken in *L. acerosus*.

Various emphases have been previously laid on these various morphological characters in an attempt to separate the two species, although no attempts have been made to utilize epidermal characters. Renier (M. S. in Crookall 1964, p. 312)



TEXT-FIG. 4. *Lepidophloios acerosus* Lindley and Hutton. A, BMNH V33591 showing undeflected leaf cushions, $\times 3$. B, IGSLds RC 1778 showing deflected leaf cushions, $\times 3$. C, cushion cuticle from above the leaf scar of V33591, $\times 400$; slide no. V33591a. D-G, cuticle from RC 1778, $\times 400$. D, cushion cuticle from below leaf scar; slide no. PL 279. E, cuticle from cushion edge; slide no. PL 282. F, cushion cuticle from below leaf scar; slide no. PL 279. Arrows directed parallel to the vertical axis of the cushion. G, ligule pit cuticle; slide no. PL 280.

believed the positioning of the ligule pits to be the most important feature while Němejc (1947, p. 78) stressed the relative lengths of the cushions and the presence or absence of keels. In contrast to these, Jongmans (1930) suggested that *L. acerosus* might represent young stems of *L. laricinus* and Stockmans and Willière (1953) similarly believed them to be conspecific. The two species are distinct, but it is certainly better to use more than one cushion character for differentiation, for, as Němejc (1947) and Crookall (1964) have already shown, individual characters are neither always well marked nor constant. The wide range of cushion characters quoted by Crookall is, however, unacceptable and I have here included many of his examples as other species.

L. acerosus has been confused with other species, a problem which has been accentuated by misinterpretation of cushion orientation. Specimens have been figured inverted, as indeed have been specimens of *L. laricinus*. *L. acerosus*, if figured upside-down (e.g. Arber 1914, pl. 28, fig. 20; Kidston 1917, pl. 2, fig. 5; Crookall 1929, pl. 22, fig. k; 1964, pl. 79, fig. 5), could be mistaken for a species of *Lepidodendron*. This could then account for Němejc's (1934) view that there was no difference between *Lepidodendron dichotomum* Sternberg and the figures published for *Lepidophloios acerosus* by West European authors. He thus believed the two species to be closely allied, if not identical, although he did later revert to giving them as distinct species (Němejc, 1946, 1947). A similar confusion seems to have arisen when Weiss (1871) joined *Lepidodendron brevifolium* Ettinghausen (1854) with parts of the *Lepidophloios laricinus* of Goldenberg (1862) and Schimper (1870) under his new name *L. carinatus*. Kidston (1886) then referred *L. acerosus* and *Lepidostrobus pinaster* Lindley and Hutton to *Lepidophloios carinatus* Weiss although he later included all in his synonymy for *L. acerosus* (Kidston 1893b, 1894). *L. pinaster* seems to be correctly reidentified as *L. acerosus* but mistakenly believed to be inverted. Jongmans (1929) and Crookall (1964) also appear correct in maintaining that *L. brevifolium* is a species of *Lepidodendron* and that it should therefore be excluded from *Lepidophloios acerosus*.

Lepidophloios macrolepidotus Goldenberg

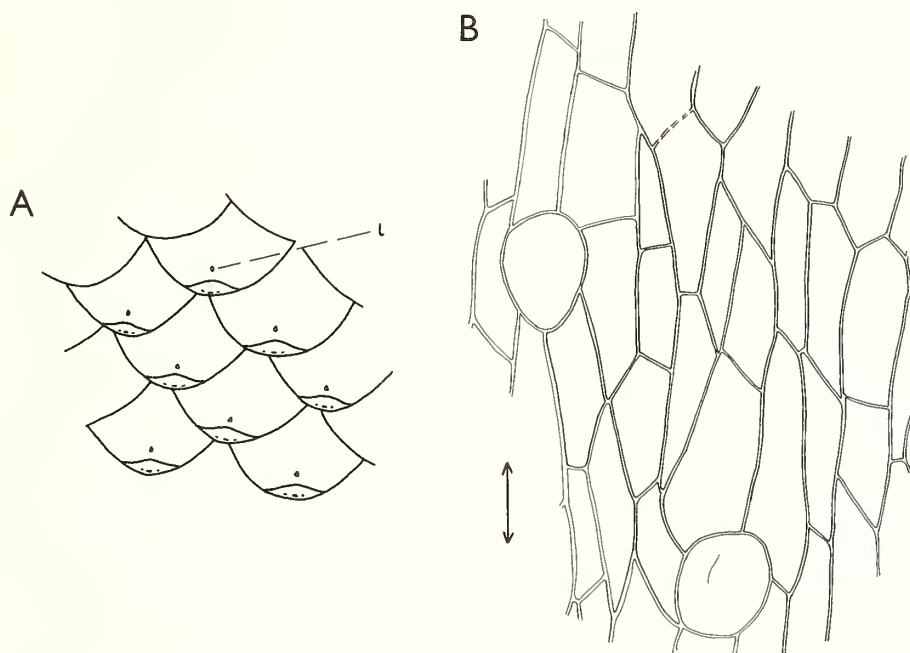
Plate 35, figs. 3–6; text-fig. 5

- 1855 *Lomatophloios macrolepidotum* Goldenberg, p. 22.
- 1862 *Lepidophloios macrolepidotum* Goldenberg, p. 37, pl. 14, fig. 25 (inverted).
- 1870 *Lepidophloios macrolepidotus* Goldenberg; Schimper, p. 52.
- 1882 *Lepidophloios macrolepidotus* Goldenberg; Renault, pars, p. 45, fig. 2 (inverted) not fig. 4.
- 1890 *Lepidophloios macrolepidotus* Goldenberg; Seward, pl. 3, figs. 1–4.
- 1899 *Lepidophloios macrolepidotus* Goldenberg; Potonié, p. 235, fig. 223.
- 1959 *Lepidophloios macrolepidotus* Goldenberg; Remy, p. 83, fig. 81.
- 1964 *Lepidophloios laricinus* Sternberg; Crookall, pars, p. 307, pl. 78, fig. 1 (inverted).
- 1967 *Lepidophloios macrolepidotus* Goldenberg; Chaloner, p. 571, fig. 390.

Material. K 3256–3257, and IGS Lond RC 2910 from above the Fenton Coal, Dodworth Colliery, near Barnsley, Yorkshire—communis Zone, Westphalian A; K4392 from above the Halifax Hard Bed, Fieldhouse Colliery, Deighton, Yorkshire—lenisulcata Zone, Westphalian A.

The largest slab of bark was K 3257, being 180 mm broad, which also had the largest leaf cushions of average visible length 16 mm and breadth 25 mm. All the

specimens, however, have leaf cushions of roughly comparable size and shape, being all broader than long with flattened surfaces possessing no keels. The leaf scars have three obvious prints in their lower halves, while the conspicuous ligule pit apertures are triangular in outline and are clearly separated from the leaf scars. The specimens also show a few cushions which appear to be separated from each other, but this is really an illusion caused by narrow strips of adhering shale which can be removed showing the cushions to be continuous and overlapping in the normal manner. Goldenberg (1862) and Renault (1882) figured similar specimens



TEXT-FIG. 5. *Lepidophloios macrolepidotus* Goldenberg, K. 3256. A, leaf cushions, $\times 1$, l—ligule pit aperture. B, cushion cuticle, $\times 400$. Arrows directed parallel to the vertical axis of the cushion; slide no. PF 2897.

with cushions separated by bands of what appear to be bark, but these could again be only overlying strips of rock matrix.

Cuticle was prepared from K 3256–3257, and IGSLond RC 2910 but as K 4392 has but a single leaf cushion it was thought unwise to remove any of its compression.

Cuticle description. The epidermis is the same on the exposed and hidden cushion surfaces. Epidermal cells are longitudinally elongated, about $30\text{--}60\text{ }\mu\text{m} \times 10\text{--}15\text{ }\mu\text{m}$ large, often with pointed ends. Anticlinal walls are straight, smooth, and $1\text{ }\mu\text{m}$ thick and the periclinal walls are flat and smooth. Stomata are about 50 per mm^2 , of average size $40\text{ }\mu\text{m} \times 30\text{ }\mu\text{m}$, and possessed superficial guard cells. No ligule pit cuticles could be prepared.

Comparison. Kidston (1893a, p. 80; 1911, p. 151) suggested that *L. macrolepidotus* was a larger form of *L. laricinus* and Crookall (1964, p. 310) doubtfully united the

two. All the described specimens of *L. macrolepidotus* seem to be of large slabs of bark presumably coming from the main trunk or large branches; but while accepting that there were possibly smaller branches bearing smaller leaf cushions it is not yet proven that these were necessarily of the *L. laricinus* kind. *L. macrolepidotus* has leaf cushions which are more flattened than those of *L. laricinus* and they possess ligule pit apertures which are more distinct and relatively more separated from the leaf scars. The epidermal cells are about the same size in the two species but the anticlinal walls are thicker in *L. laricinus* ($2\text{ }\mu\text{m}$) than in *L. macrolepidotus* ($1\text{ }\mu\text{m}$). *L. laricinus* has 250 stomata per mm^2 with guard cells in pits ($6\text{--}10\text{ }\mu\text{m}$ deep) but *L. macrolepidotus* has less stomata (50 per mm^2) and superficial guard cells.

The 'young branches' figured by Renault (1882, fig. 4) are excluded from this species in agreement with Kidston (1893*b*) and Crookall (1964). They seem to be more like *L. acerosus* or to a very similar species. The specimen described by Kidston (1893*b*) from the lower Carboniferous of Scotland is also excluded and described here as the holotype of *L. grangeri* sp. nov.

Lepidophloios grangeri sp. nov.

Plate 36, figs. 1-4; text-fig. 6

1893*b* (?) *Lepidophloios macrolepidotus* Goldenberg; Kidston, p. 560.

1964 *Lepidophloios laricinus* Sternberg; Crookall, pars, p. 310, pl. 74, fig. 6 (inverted).

Material. Holotype, K 1828 from above the Craw Coal, No. 4 Mine, Grange, Boness, Linlithgowshire—within the Limestone Coal group of the Carboniferous Limestone Series of the Namurian (D_3 Coral brachiopod Zone and E_1 age of the goniatite notation, according to Macgregor in Trueman 1954).

The type specimen, which is the only known one referable to this species, is a 100 mm broad slab of compressed bark on an ironstone nodule. Cuticle was easily obtained from the exposed upper cushion surfaces but could not be prepared from the overlapped underlying lower surfaces. The ligule pit cuticles were unfortunately very cracked and only small fragments were therefore obtained.

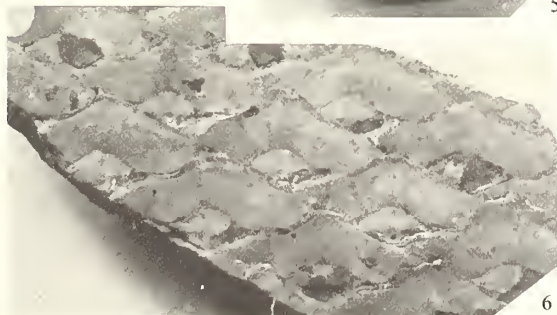
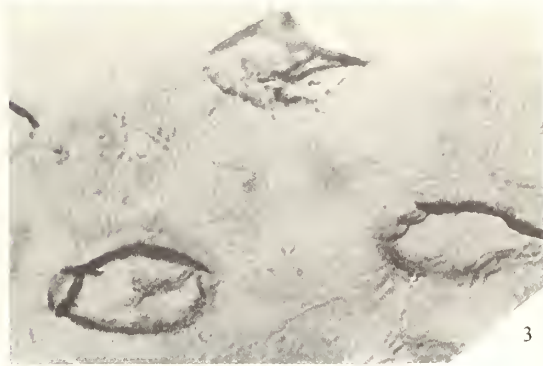
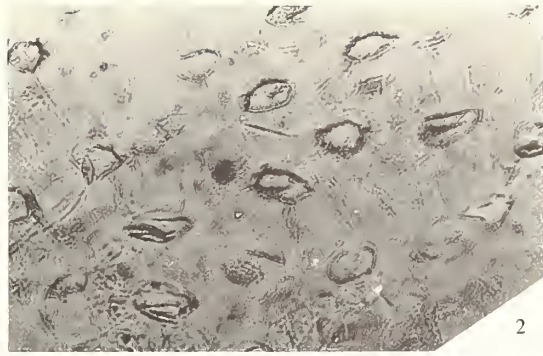
Diagnosis. Exposed portions of leaf cushions broader than long. Ligule pit apertures adjacent to upper angles of leaf scars. Cushion surface smooth with no keel. Epidermal cells from central area of cushion longitudinally elongated, about $60\text{--}70\text{ }\mu\text{m} \times 15\text{ }\mu\text{m}$ large. Epidermal cells from sides of cushion roughly isodiametric, $15\text{--}20\text{ }\mu\text{m}$ large. Anticlinal walls straight, smooth, $1\text{ }\mu\text{m}$ thick. Periclinal walls flat, smooth. Stomata about 150 per mm^2 over the whole cushion surface; average size $40 \times 25\text{ }\mu\text{m}$. Guard cells level with epidermal surface. Ligule pit about $230\text{ }\mu\text{m}$ broad; lining cells rectangular, longitudinally elongated, about $45\text{--}55\text{ }\mu\text{m} \times 12\text{ }\mu\text{m}$ large.

Derivation of name. From the type locality.

EXPLANATION OF PLATE 36

Figs. 1-4. *Lepidophloios grangeri* sp. nov. 1, K 1828 from above the Craw Coal, No. 4 Mine, Grange, Boness, Linlithgowshire, $\times 2$. 2, 3, cushion cuticle, slide no. PF 2900. 2, $\times 200$; 3, $\times 600$. 4, ligule pit cuticle; slide no. PF 2898, $\times 100$.

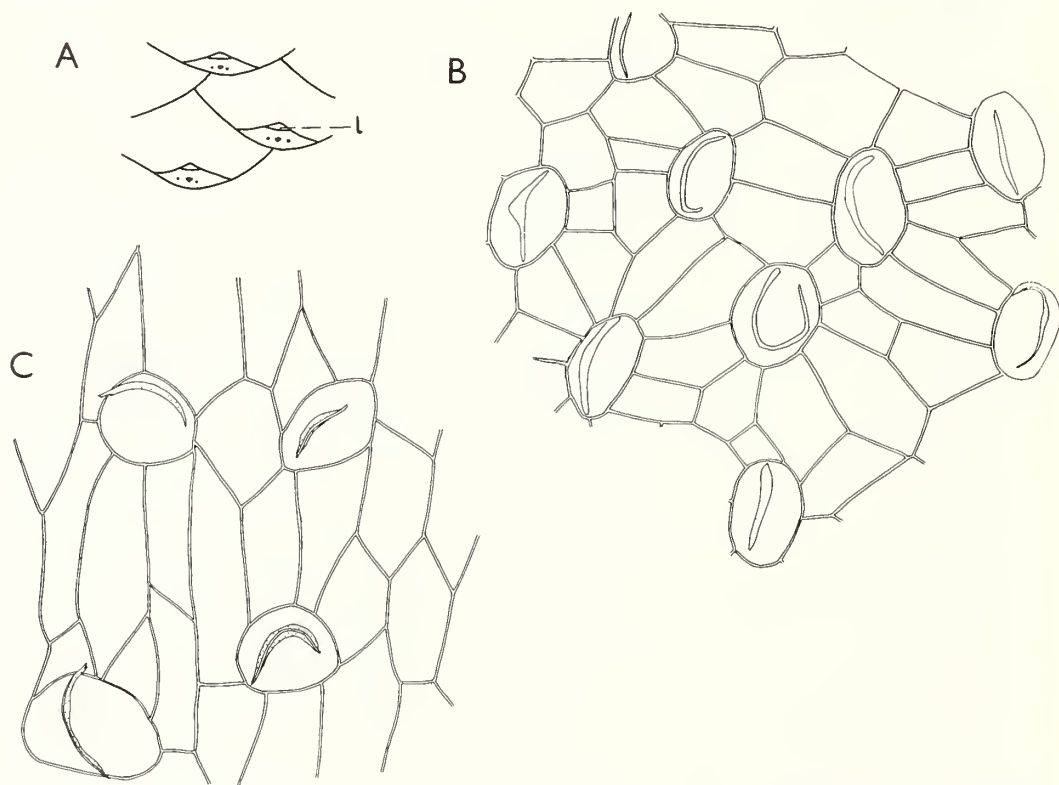
Figs. 5-7. *Lepidophloios acadianus* Dawson from Joggin Mine, Nova Scotia, Canada, 5, K 2318, $\times 0.5$. 6, K 2323, $\times 1$. 7, cushion cuticle from K 2323; slide no. PF 3131, $\times 200$.



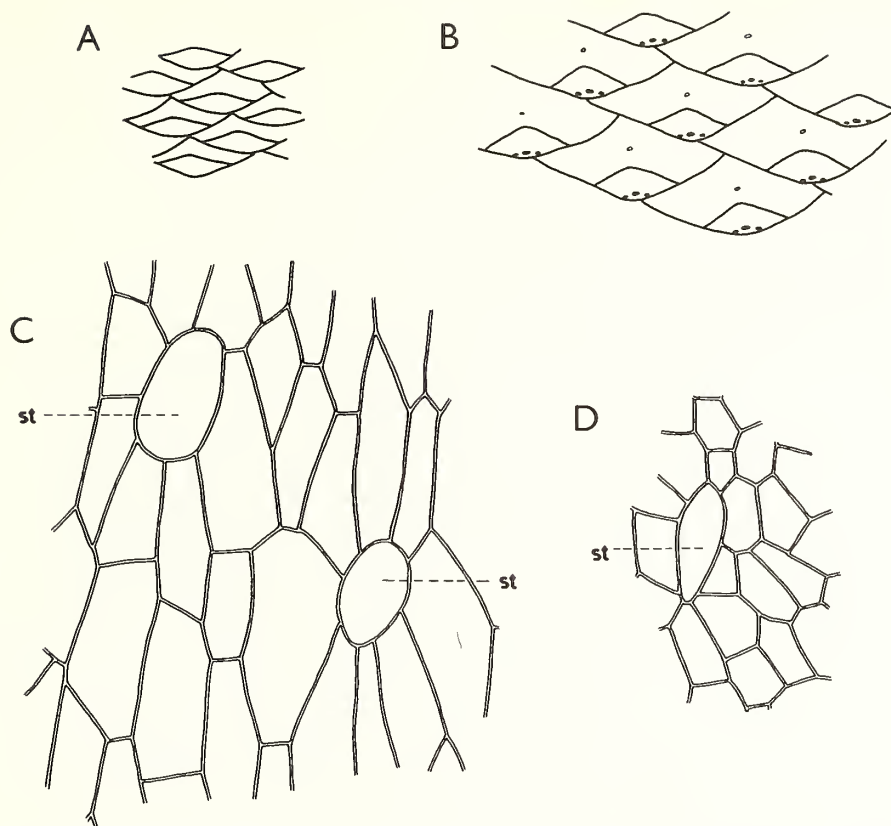
Comparison. The type specimen has been included within *L. macrolepidotus* and *L. laricinus*, but it can be distinguished from both of these species on cushion morphology and cuticle characters. The ligule pit aperture is adjacent to the leaf scar in *L. grangeri* but is clearly separated from the scar in the other two species. The epidermis has elongated cells in the central area and isodiametric cells on the lateral portions so it is similar to that of *L. laricinus*, but different to that of *L. macrolepidotus* which has only elongated cells. *L. laricinus* differs in having shorter cells in the central region even though the cells from the lateral areas are of comparable size to those in *L. grangeri*.

The stomata are of comparable size in all three species, but their frequencies differ. They are 150 per mm² in *L. grangeri*, 50 per mm² in *L. macrolepidotus*, and 250 per mm² in *L. laricinus*. The guard cells are also sunken in pits in *L. laricinus* whereas in the other two they are superficial.

L. grangeri also differs from the other species of *Lepidophloios* described here in coming from the Lower and not from the Upper Carboniferous. The other Lower Carboniferous species, *L. scoticus* Kidston, has been shown to possess a variety of leaf cushion sizes and shapes, but none is really like those of *L. grangeri*. The largest



TEXT-FIG. 6. *Lepidophloios grangeri* sp. nov. K 1828. A, leaf cushions, $\times 1$. l—ligule pit aperture. B, C, cushion cuticle, $\times 400$; drawn from the undersurface. B, cuticle from the non-median areas; slide no. PF 2900. C, cuticle from the median areas; slide no. PF 2899.



TEXT-FIG. 7. *Lepidophloios acadianus* Dawson. A, K 2324, $\times 1$. B, K 2323, $\times 1$. C, D, cushion cuticle from No. 2323, $\times 400$, st—stomata. C, cuticle from the median area of the cushion; slide no. PF 3131. D, cuticle from the non-median area of the cushions; slide no. PF 3132.

cushions of *L. scoticus* have exposed areas which are longer than broad in contrast to those of *L. grangeri*. The lower edges of the leaf scars are also much flatter and the ligule pit apertures are separated from the leaf scars. No cushion cuticles have yet been described from *L. scoticus* so no comparison can be made of epidermal features, but even without this additional information the two types of cushion appear sufficiently different for species distinction.

Lepidophloios acadianus Dawson

Plate 36, figs. 5-7; text-fig. 7

1866 *Lepidophloios acadianus* Dawson, pp. 163, 168, pl. 10, fig. 45.

1868 *Lepidophloios acadianus* Dawson, p. 489; text-fig. 171.

1888 *Lepidophloios acadianus* Dawson, p. 166; text-fig. 44.

Material. K. 2318-2324 from Joggin, Canada.

All seven specimens were identified by Dawson as *L. acadianus* and K 2324 is labelled as 'fragment of type'. The exposed areas of the downturned cushions are

all broader than long, with the leaf scars at their extreme bases except in K 2318 where a small portion of the cushion can be seen below the scars. Cushion surfaces are flat with no keels and the ligule pit apertures are clearly separated from the leaf scars.

Cuticle description. The epidermis is the same from the cushion surfaces above and below the leaf scars. The epidermal cells on the central areas of the cushions are elongated longitudinally and are $40\text{--}70\text{ }\mu\text{m} \times 18\text{--}30\text{ }\mu\text{m}$ large, while the cells on the cushion are roughly isodiametric and about $15\text{ }\mu\text{m}$ large. Stomata are about 130 per mm^2 and of average size $45\text{ }\mu\text{m} \times 33\text{ }\mu\text{m}$. The guard cells are usually level with the epidermis but are occasionally sunken in $3\text{ }\mu\text{m}$ deep pits.

Comparison. Dawson published three identical accounts of this species but figured the leaf cushions upside down and without ligule pits. He believed *L. acadianus* to be closely allied to *Ulodendron majus* Lindley and Hutton and *L. laricinus* Sternberg; while Kidston (1901, p. 158), Bell (1944, p. 93), and Crookall (1964, p. 311) believed it to be conspecific with *L. laricinus*. *U. majus* is a completely different type of stem which possess permanently attached leaves and not downwardly directed leaf cushions (Thomas 1967*b*) so it has little in common with this species. *L. laricinus* is naturally similar, but can be distinguished by both cushion morphology and cuticle characters. The exposed parts of the cushions are relatively narrower with more rounded lower angles, the foliar prints are relatively higher on the leaf scars and the ligule pits are more distinct. *L. laricinus* also has larger epidermal cells, more stomata than *L. acadianus*, and the guard cells are normally sunken in pits.

DISCUSSION

Lepidophloios, like the other genera of arborescent lycopods, has been interpreted differently by various authors. Confusion and differences of opinion have existed over the range of species variation and over the very number of species which were thought to exist. Previous workers have used just leaf cushion morphology to identify their specimens, but recent work on other genera (Thomas 1967*a, b*, 1970) has shown how epidermal characters are clearly of immense value for this purpose. Therefore epidermal cell sizes and shapes, stomatal sizes, numbers, and distributions were studied in a range of species to see if they were similarly useful in this genus.

L. laricinus and *L. acerosus* are the two commonest species which are relatively easily distinguished on a combination of cushion characters, but at times they have been thought to be conspecific and have been also linked with other species of *Lepidophloios* and even *Lepidodendron*. Clearly the differences in cushion morphology can be thought to be insufficient for species distinction so there is some divergence of opinion here. However, if one takes the two 'recognizable forms' and looks at their epidermal details there are additional characters available for comparison. In this instance, such extra information clearly points to a continued separation of the two species. Similar epidermal evidence indicate that *Lepidophloios macrolepidotus*, *L. grangeri*, and *L. acadianus* are recognizable as distinct species and can not be thought of as growth forms of *L. laricinus* as has been often suggested.

Epidermal studies are thus once again of great value and the information gained

has helped to crystallize a better idea of the various species. It has hopefully provided a sounder basis for understanding the range of species variation and for identifying new material.

The other important aspect of this type of study is that it should allow us to recognize growth forms of the various species. Previous work by Walton (1935), Andrews and Murdy (1958), and Eggert (1961) has suggested that *Lepidodendralea* trees grew by dichotomizing apices which progressively diminished in size. Therefore shoot diameter is no indication of age for the smaller shoots were merely more terminal and were not young shoots which had not yet enlarged by large amounts of secondary thickening, i.e. large shoots were formed from large apices while small shoots were formed from small apices. Some secondary thickening did occur but only in a manner which seems to have accentuated the primary growth form, for apparently the trunk and main branches were thickened much more than the smaller terminal shoots. Leaf growth also varied proportionally to shoot diameter, so in both *Lepidodendron* and *Lepidophloios* the narrower branches have smaller leaf cushions while only the very terminal shoots seemed to retain the distal foliage parts of their leaves. There are, however, certain major differences which existed between these two genera regarding the effects of limited secondary growth on the leaf cushions. Shoot expansion in *Lepidodendron* apparently did not initially affect the actual leaf cushions, but separated them instead by a gradual growth of the intercushion areas (Thomas 1966). In *Lepidophloios*, however, the situation appears to be rather different for the leaf cushions apparently never separated as in *Lepidodendron*. Those specimens suggesting such a separation (e.g. *Lepidophloios macrolepidotus*) have now been shown to be rather different with the intercushion areas being really narrow strips of shale protruding from between the overlapping leaf cushions. Instead of separating, the cushions appear to have enlarged and bulged further outwards and downwards. Indeed, the specimens of *L. acerosus* discussed above indicate that the cushions were originally of the *Lepidodendron* type. Then by expansion they would have bulged outwards and downwards synchronously with the enlargement of the shoot. Obviously much more evidence is needed to clarify our ideas of this particular method of growth and it would be much better if such stages could be demonstrated in species other than *Lepidophloios acerosus*. Unfortunately we are dealing with growth stages and this is always a major problem, because it is the growing points which are the least likely to become fossilized.

The other point of interest which centres around such a peculiar type of shoot growth is the usefulness of cushion enlargement to the growing plant. The question of photosynthetic efficiency of the arborescent lycopods has been broached several times but not in direct relationship to *Lepidophloios*. Andrews and Murdy (1958) and Andrews (1961) thought these plants possessed relatively small amounts of photosynthetic tissue because only the smallest twigs retained their leaves. Then the demonstration of numerous stomata on the leaf cushions suggested that the stems were much more photosynthetic than previously thought (Thomas 1966). While Chaloner and Collinson (1975) have since shown that *Sigillaria* possessed even more stomata per unit area than *Lepidodendron* and suggested that the increased amount of potential photosynthetic activity might help to explain their ability to grow with only a crown of leaves. What we may see in *Lepidophloios* is a further attempt to

increase the photosynthetic ability of these plants, for such an increase in cushion size would appear to result in the production of more photosynthetic tissue. Perhaps we could take this to be the very reason for leaf cushion enlargement and the evolutionary change from the *Lepidodendron* type of cushion.

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ZYGOSPIRA AND SOME RELATED ORDOVICIAN AND SILURIAN ATRYPOID BRACHIOPODS

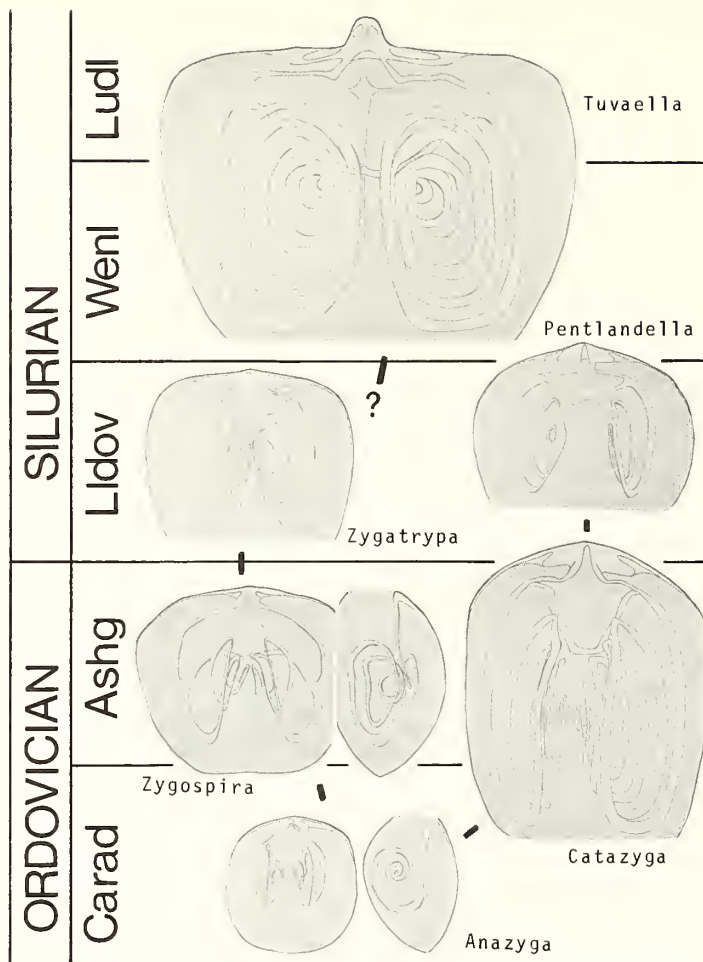
by PAUL COPPER

ABSTRACT. The Zygospiridae are redefined to include 'primitive' atrypoid brachiopods with dorsally to dorso-medially directed spiralia, normally with fine ribs and a one-piece jugum dorsal to the spiralia. The Ordovician-Silurian family is divided into three: Zygospirinae, Catazyginae (new sub-fam.), and Tuvaellinae. Internal structures of *Zygospira*, *Anazyga*, *Catazyga*, *Pentlandella*, and *Tuvaella* are evaluated in terms of their evolutionary significance. A new genus *Zygatrypa* is erected. *Eospirigerina*, which was probably derived from zygospirid stock in the late Ordovician, differs in having ventrally located, separated jugal processes and trends towards 'frilly' shells: this represented a major jump towards a postulated *Zygospiraella*-*Protatrypa*-*Gotatrypa* lineage. In late Caradoc-Ashgill times *Catazyga* inhabited deeper water, whereas *Zygospira* lived in shallow-water communities. The Clintonellinae, including *Alispira*, are tentatively assigned to the Atrypidae, with Silurian taxa such as *Nalivkinia* and *Anabaria*.

INTERNAL structures of many of the earlier ribbed atrypoids belonging to the family Zygospiridae, which first appeared in Caradoc time, are not generally well known. The pioneering morphological work of Hall (1862, 1893), Davidson (1882), and Schuchert (1893) on the zygospirids has not been corroborated or used in classifications, except in the broadest sense. Data is lacking on apical shell structures (deltidial plates, 'dental plates', pedicle collars, etc.) and brachidial structures (socket plates, crura, jugal processes). It is the intent of this paper to fill in some of the gaps in our knowledge of the group, so as to determine generic variation and evolutionary trends. The taxa *Anazyga*, *Zygospira*, and *Catazyga* form the centre of this study, but some related ribbed atrypoid genera are also examined. Serial sections demonstrate the affinities of *Pentlandella*, *Tuvaella*, *Alispira*, 'Clintonella', *Nalivkinia*, and *Anabaria*. The first two are retained within the zygospirids, but the others are removed. *Zygospiraella* is interpreted as an ancestor of the *Protatrypa*-*Gotatrypa*-*Atrypa* lineage: this will be described in a subsequent paper. Smooth Ordovician spire-bearing genera, such as *Protozyga*, *Idiospira*, and *Cyclospira*, are not within the scope of this paper, but are also under revision.

EVOLUTION

The main bloom of the group took place during the late Caradoc and Ashgill, but by latest Ordovician time the zygospirids in eastern North America and western Europe had been replaced by *Eospirigerina*. During this interval, and in the early Llandovery in this region, there appears to be no trace of any zygospirids. Nevertheless, by Upper Llandovery (Telychian) time, two zygospirids reappear, *Pentlandella* in Britain and Estonia, and *Zygatrypa*, described herein from Anticosti Island. *Tuvaella*, from the Tuva region of Asian U.S.S.R. and Mongolia, also appeared in



TEXT-FIG. 1. The most important evolutionary trends in the Zygospiridae lie with the disposition and nature of the spiralia and the jugum. The spiralia tend to produce increased numbers of whorls, a change from medially to dorsally directed coils, and the jugum shifts in position from an anterior to a posterior location with an eventual position near the pedicle valve. These trends probably reflect more efficient suspension feeding and changes in the location of the digestive tract.

late Llandovery or early Wenlock time, but was endemic to that area. *Tuvaella* ranged into late Silurian time (Pridoli?), and appears to have been the last-surviving zygospirid.

The origin of the earliest atrypoids is unclear. If *Protozyga* is the common ancestor, a smooth impunctate prototype form is indicated, possibly a camerellid or smooth rhynchonellid. However, if *Protozyga* represents an offshoot from *Anazyga*, a ribbed rhynchonellid, or even an orthid, may be the root-stock. We are no closer to an answer than at the time of Cooper's monograph on the Chazyan brachiopods (1956).

The geological succession in Ontario is for *Protozyga* to appear first, followed by *Anazyga*, then *Zygospira* and *Catazyga*.

A general trend in the Zygospiridae is towards increasing size in all three sub-families, for example, *Zygospira* itself reached maximum width in Ashgill time and the largest catazyginids are late Ordovician *Catazyga*. However, *Zygatrypa* and *Pentlandella*, offshoots of Ordovician genera, are very small by comparison and appear to show a reversed late trend towards decreasing size and finer ribbing. The origin of *Tuvaella* lies in the Zygospiridae, but perhaps not with *Zygatrypa*. *Tuvaella* is the largest known zygospirid, reaching widths of some 60 mm with *T. gigantea* Chernyshev in late Silurian time (Vladimirskaia 1972). Even 'large' late Ordovician zygospirids such as *Catazyga* and *Zygospira* rarely exceed 15 mm. Another trend is rib coarsening in the zygospirinids, leading from *Anazyga* to early *Zygospira* and late *Zygospira* in the Ordovician, and also in the *Catazyga* group. However, in Silurian time, the zygospirids tend to be very fine ribbed, except for *Tuvaella*. A reverse trend, towards loss of ribs, may have occurred in some catazyginids. Ulrich (1888, pp. 196–197) described a late Ordovician species of catazyginid, which he called *Glassia schuchertana*, because ribs were barely, if at all, visible on many well-preserved specimens. Foerste (1910) assigned it to *Catazyga*, as did Meek (1873) who identified it as the same as the type species of *Catazyga*, *C. headi* (Billings 1862). Silurian *Pentlandella* from Estonia also possess such fine ribs that these are frequently not visible on parts of the anterior shell. It is possible that the loss of ribs resulted in the appearance of *Glassia* in Llandovery time, since the spiralia in *Glassia* are medially directed, as in *Catazyga*.

Internal trends differ in individual sub-families but are probably more significant. *Anazyga* has a fused jugum located antero-dorsally to the cone axes, and the spiralia are medially directed (cone axes parallel or near parallel to the commissural plane). Its descendant *Zygospira* has a dorsal jugum located at the cone axes, or posterior to the cone axes, and spiralia directed dorso-medially (cone axes some 45° from the commissural plane). If the two taxa form a continuous lineage from Caradoc through Ashgill time, then the jugum migrated from an anterior position to a posterior position and the cone axes rotated some 45° from the commissural plane in a dorsal direction. In addition, the same lineage shows an increasing trend from only one or two spiralian whorls in *Anazyga* to three to five in *Zygospira*. It is perhaps significant that in the Atrypidae of the Siluro-Devonian, thirty or more spiral whorls are known and the separated jugal processes are located antero-ventrally. *Eospirigerina* in the late Ordovician Ellis Bay Formation of Anticosti Island has eight to nine spiral whorls and unconnected jugal processes located antero-ventrally. This clearly separates *Eospirigerina* from the Zygospirinidae, from which it must have evolved. The dorso-medial turning of the cone axes culminated in almost full dorsal directions in the latest Ordovician (text-fig. 1). It is significant that the location of the jugum in the Zygospiridae is dorsal: the jugum is derived from the initial whorl of the spirallium but is directed dorsally and lies very close to the median septum of the brachial valve, frequently arching over it. This implies that the jugum may have rested or been suspended over the brachial valve floor. The jugal processes in the Atrypidae and Palaeferellidae are ventral, i.e. the jugal process is located ventrally and posterior to the spiralia and thus lies closest to the pedicle valve. Thus not only

do these other families differ in having a divided jugum, or jugal processes (Copper 1967), but the implication is that if the jugum-jugal processes held mouth parts, their feeding processes would be quite different.

In the Catazyginae there are different internal trends. *Catazyga* probably evolved from *Anazyga* in the late Caradoc. It is uncertain whether to assign *Anazyga* to the *Catazyga* group or to the *Zygospira* group. Externally *Anazyga* is closer to *Zygospira* in its wider shell, fold-sulcus, and beak structure. Internally it could belong to either, except that *Anazyga* has dental cavities, like *Zygospira*, and *Catazyga* has none. If *Catazyga* evolved from *Anazyga*, as seems most likely, then this involved a loss of dental cavities and great thickening of the pedicle valve anteriorly. *Catazyga*, and its Silurian descent *Pentlandella*, both retain spiralia which are strongly directed towards the centre of the shell. The cone axes show a lesser rotation from the commissural plane than in the zygospirinids. *Catazyga* has about seven spiral whorls. Rubel (1970) recorded four whorls for Estonian *Pentlandella*, but an adult specimen sectioned for this paper, from the same Estonian locality, revealed only two (text-fig. 7). Since Silurian *Pentlandella* are about half the size of Ordovician *Catazyga* this does not necessarily reflect an independent evolutionary reduction in spiralia, but is probably a size-related factor.

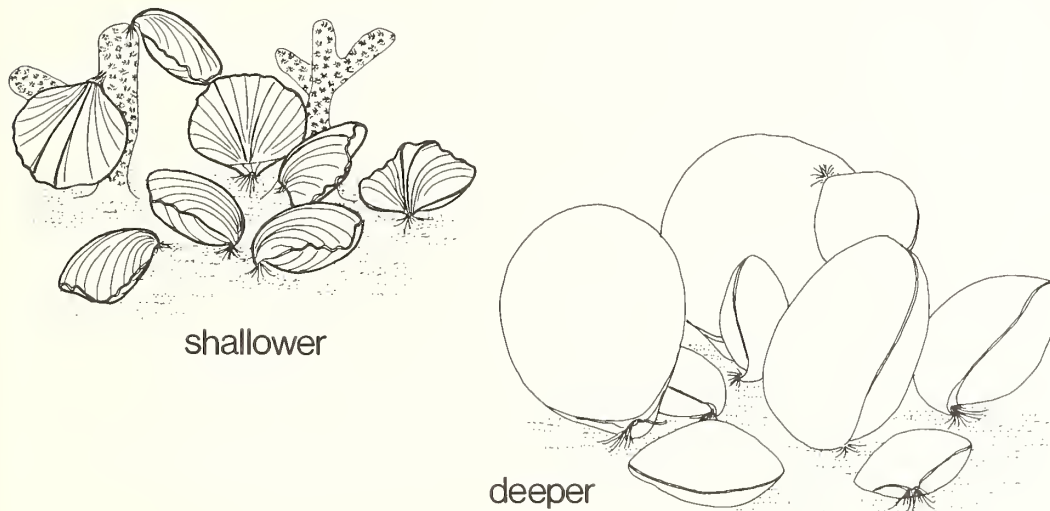
The structure of the jugum and spiralia in Silurian *Zygatrypa* is similar to that of *Zygospira*, except in the location of the jugum. In *Tuvaella rackoviskii* from the Tuva region and Mongolia (text-fig. 14) no dental cavities are present, but the jugum is located dorsally and its central point lies close to the cone apices. This is like other zygospirinids. Functionally this suggests that the central part of the jugum held a mouth organ to which food currents were canalized. The cone axes are directed as in *Zygospira*, and five to eight whorls were present. In later *T. gigantea*, Vladimirskaya (1972) recorded up to ten whorls, which seems to be a maximum figure for any Zygospiridae. It is possible that the family gave way to the Atrypidae and other groups because these had the ability to use larger numbers of spiral whorls and were thus more efficient filter feeders.

THE ORDOVICIAN-SILURIAN BOUNDARY

Atrypoid brachiopods of the transitional period from Ordovician to Silurian time are not well known. In the Anticosti section in eastern Canada, which holds a richly fossiliferous suite of rocks straddling the 'boundary', the zygospirids were halted in the Vaureal Formation and do not continue into the Ellis Bay Formation, most of which (on the basis of brachiopods, rugose and tabulate corals, and stromatoporoids) is still in the Ordovician. I agree with Bolton (1972) that the base of the Becscie Formation with *Zygospiraella* (Atrypidae) corresponds very closely to the boundary. The zygospirids, therefore, are not of great value in eastern North America in determining the boundary. They were in decline some time before the close of the Ordovician, with only two conservative lines maintained as rare elements in the Llandovery (*Pentlandella* and *Zygatrypa*).

Amsden (1971) described a transitional fauna from the Edgewood Formation of Illinois and Missouri including '*Eospirigerina*' *putilla* (Hall and Clarke, 1893), which is said to be present in the latest Ordovician as well as early Llandovery.

This species may be a true *Zygospira*, as described by the original authors, and needs redescription. *Eospirigerina* is so abundant in the Ellis Bay Formation of Anticosti Island that it forms distinctive shelly horizons; several species are present. The species group of '*Plectatrypa*', is readily confused with *Eospirigerina* in the late Ordovician (but not in the Silurian of Western Europe). '*Eospirigerina*' *hibernica* Reed (1932) from Northern Ireland is a late Ordovician form first figured by Portlock (1843, pl. 37, fig. 4). '*Plectatrypa*' *partita* (Sowerby, 1839) from Goleugod Hill (Lower Llandovery) in Wales is a similar early Silurian form. The *Eospirigerina*–'*Plectatrypa*' group is complex but could perhaps shed light on the boundary problem. *Zygospiraella* at present is the most useful atrypoid indicator of early Llandovery age.



TEXT-FIG. 2. During Ashgill time, zygospirids were dominant in two assemblages; a shallower-water *Zygospira* assemblage with bryozoans, tabulates, and colonial rugose corals, and a deeper, quiet water assemblage of *Catazyga* and sowerbyellids (examples drawn from *Z. modesta* and *C. headi*; no ribs drawn on latter). Scale $5/3\times$.

PALAEOECOLOGICAL DISTRIBUTION

The earlier zygospirids *Protozyga* and *Anazyga* were probably moderately deep-water benthos. Their common occurrence is in dark-grey to black calcareous shales or muddy limestones. Common associates of *Anazyga* are other small brachiopods, small hemispherical colonies of *Prasopora* and ostracodes. *Anazyga* does not occur abundantly with bioherms or biostromes with stromatoporoids, tabulate or rugose corals, or with digitate bryozoans in higher energy, shallow-water zones. By later Ordovician time, zygospirids were ecologically sorted into two communities or habitats: *Zygospira* with coarser ribs, well-defined fold-sulcus, and planoconvex-ventribiconvex shells, lived in a shallow-water community with bryozoans (Bretsky 1969; Richards 1972), and *Catazyga* in a deeper-water, muddy environment, frequently nearly barren of anything but crowded catazygid nests (text-fig. 2). The

two genera rarely occur together except in ratios of 100:1 or more. In the Vaureal Formation on Anticosti Island *Zygospira* is apparently absent and *Catazyga* is abundant. Towards Manitoulin Island, some 400 miles westwards, *Zygospira* is locally extremely abundant but *Catazyga* occurs only in isolated patches. A similar presence-absence occurrence is described from Indiana and Ohio by Richards (1972, p. 402). The two taxa seem to be reliable relative depth indicators, but at present actual depths are problematical. It is possible that *Zygospira* represented the depth equivalent in the Silurian of the *Pentamerus-Eocoelia* community and *Catazyga* the equivalent of the *Clorinda* community (Ziegler 1965).

The mode of life of many zygospirids is hypothetical. *Zygospira* has a small, but distinctive, interarea and anacline beak in maturity, with young specimens having a proportionally larger interarea and apsacline-orthocline beak. This suggests a pedicle-attached mode of life, particularly in early growth stages. However, some gerontic specimens have hypercline beaks, which would have made a functioning pedicle difficult in later growth stages. Richards (1972) has shown the clustering of zygospirids around bryozoan finger-colonies and this may have been a common association. In mass occurrences of zygospirids, bryozoans are too rare to have served as more than an occasional anchoring site: the zygospirids probably attached to each other, young to living parent shells or to vacant shells on the sea bottom. Richards noted that *Zygospira* often appears to have settled on live substrates (other benthos), and may have been a pioneering species in substrate colonization. This is possible; in one outcrop on Manitoulin Island heavy concentrations of *Zygospira* preceded a biostrome. Life assemblages of *Zygospira* show that the shell usually attached itself with its lateral commissure at an angle to the host or substrate, and with the brachial valve on the downward or host-ward side. This would mean that the spiralia would be orientated in the same direction (downwards or host-wards and inwards). Food currents created by the lophophore would have been taken in through the sides of the shell and released anteriorly.

Catazyga, with a hypercline beak in maturity, biconvex-ventri-biconvex shell and weak fold-sulcus, is rather different in its usual lack of associates of any kind other than some strophomenids. Cluster accumulations, presumably nests, show that in dense clusters most shells are orientated at a relatively high angle to the substrate with the pedicle valve uppermost and the plane of symmetry tilted away from the vertical. Thus the anterior commissure, and presumably the exhalent current were further away from the substrate than with *Zygospira*. Shell elongation would accentuate this (*Zygospira* is wider: *Catazyga* longer). However, in more moderate densities of 40–60 per 100 square cm, with non-touching shells on the substrate, the *Catazyga* generally lie flat on the substrate and with the pedicle valve uppermost. What this means is not clear. Possibly with decreased densities, waste clearance away from the substrate was not such a problem, or with shells no longer touching and therefore supporting each other upright, the pedicle was too weak to maintain a near vertical or angled position. Since beak incurvature was severe in maturity, suggesting less-functional pedicles, the latter explanation may be more correct.

A reconstruction (text-fig. 2) demonstrates the postulated modes of life of the two dominant late Ordovician taxa. The catazyginids and zygospirids in the Silurian seem to have maintained essentially the same ecological polarity. *Pentlandella*

normally occurs in shales or mudstones with few other organisms and rarely with coralline skeletons. *Zygatrypa* (known only from the Silurian of Anticosti Island) is an inhabitant of the *Stricklandia* community, and occurs with *Atrypopsis*, common *Gotatrypa* and clintonellinids.

SYSTEMATIC DESCRIPTIONS

Order ATRYPIDA Rzhonsnitskaya, 1960
Family ZYGOSPIRIDAE Waagen, 1883 (emend.)
[= Anazygidae Davidson, 1883]

Primitive, smaller, planoconvex-biconvex, non-lamellose, usually tubular-ribbed atrypoids with minute pedicle openings, beaks orthocline to hypercline, no deltidial plates, or small plates. Internally the family is characterized by a fused jugum, located dorsal to the spiralia and moving in position anteriorly to posteriorly during evolution in the Ordovician. Age: Ordovician (Caradoc) to Silurian (Ludlow).

Subfamily ZYGOSPIRINAE Waagen, 1883

Here emended to include *Protozyga* Hall and Clarke, 1893, *Anazyga* Davidson, 1882, *Zygospira* Hall, 1862, *Hallina* Winchell and Schuchert, 1892, and *Zygatrypa* gen. nov.

The internal structure of *Protozyga* and *Hallina* was described, with some doubts, by Hall and Clarke (1893, pp. 149–151). *Protozyga* was figured with an anteriorly located jugum and short, one coil spiralia (ibid., p. 149) which seems correct in view of the internal morphology of *Anazyga*. *Hallina* was figured with only an anterior jugum and no spiralia (ibid., p. 151). Cooper (1956, pp. 689–690) did not define the latter genus nor find any species with spiralia. The type species of *Hallina*, from the Lebanon Formation of Tennessee, indicates a vertical distribution which in part coincides with that of *Anazyga*. *Hallina* may be a junior synonym of *Anazyga*. Externally they are not possible to differentiate; internally they both have well-defined cavities. Internals of *Hallina* need revision, but topotypic material is invariably badly preserved (G. A. Cooper, pers. comm.). The common features of the Zygospirinae seem to lie in the possession of finely ribbed planoconvex-ventribiconvex shells with a modest to sharp ventral fold-dorsal sulcus, orthocline-anacline beaks, small but visible pedicle openings, dental cavities or nuclei, thin shell walls, an anterior to posterior jugum, and medially to dorso-medially directed spiralia.

Range: Caradoc to Llandovery.

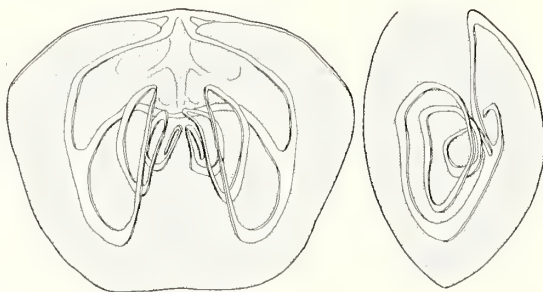
Genus ZYGOSPIRA Hall, 1862

Type species. *Atrypa modesta* (Say in Hall 1847). Say apparently identified this in collections of the Academy of Natural Sciences, Philadelphia as *Producta modesta* (ibid., p. 141).

Range. Late Caradoc (Maysvillian) to Ashgill (Richmondian).

Distribution. North America, western Europe, ?Siberian Platform, Kazakhstan. Not yet reported from South America, but should occur in Australia, in view of great similarities in associated benthic corals with North America.

Diagnosis. Moderately sized, relatively coarsely ribbed, carinate zygospirids with ventri-carinate, planoconvex shells, small interarea, orthocline-anacline beaks. Internally, dorso-medially directed spiralia with five to eight whorls and dorsal jugum located at or posterior to spiralia apices; dental cavities, small deltidial plates present. For spiralia refer to text-fig. 3.



TEXT-FIG. 3. Reconstruction of the spiralia in the type species *Zygospira modesta* based on serial sections shown in text-fig. 4. Note the nature of the jugum. Scale approx. $\times 7$.

Species assigned.

Zygospira cincinattiensis James, in Meek 1873 (p. 126, pl. 11, fig. 5a-c), basal Maysville Formation (Foerste 1910), Cincinnati, Ohio, U.S.A.

Zygospira richmondensis Caley, 1936 (p. 78, pl. 1, figs. 4, 6). Kagawong Formation, High Falls, Manitoulin Island, Ontario, Canada (Pl. 37, figs. 9-10).

Zygospira modesta kagawongensis Caley, 1936 (p. 58), Unit 8. Meaford Formation, Section no. 16, Kagawong Falls, Manitoulin Island, Ontario, Canada. Species becomes a *nomen nudum*, unless it is described and figured.

Zygospira putilla Hall and Clarke, 1893 (p. 157, fig. 150; pl. 54, figs. 35-37). Hudson River Group, Edgewood, Missouri, U.S.A. Amsden (1974) relegates this species to *Eospirigerina*.

Zygospira parva Rukavishnikova, 1956 (pp. 162-163, pl. 5, figs. 14-16). Otorsk and Dulankarin Horizons, southern Kazakhstan, U.S.S.R. Very weakly carinate.

Zygospira kentuckiensis Nettleroth, 1889 (pp. 138-139, pl. 34, figs. 21-25). 'Hudson River or Cincinnati Group', Taylor's Station, Kentucky, U.S.A. One of the largest known *Zygospira*.

Zygospira meafordensis Foerste, 1924 (p. 128, pl. 15, fig. 3a-c). 'Queenston Member, Richmond.' North-west Meaford, Ontario.

Zygospira raymondi Foerste, 1924 (p. 128), figured in Raymond (1921, p. 28, pl. 8, figs. 1-5). Collingwood Shale, Craigleath, Ontario, Canada.

Zygospira meldalensis Reed, 1932 (p. 144, pl. 22, figs. 12, 12a). Kalstad Limestone, Meldalen, Norway.

Zygospira resupinata multicostata Howe, 1965 (pp. 653-655, pl. 81, figs. 1-8). Aleman Limestone, Trans-Pecos, Texas, U.S.A.

Zygospira sulcata Howe, 1965 (pp. 655-656, pl. 81, figs. 9-12). Uppermost Upham Limestone, Lone Mountain, New Mexico, U.S.A. Finely ribbed form.

Zygospira concentrica Ulrich, 1888 (pp. 14-15, pl. 7, figs. 10, 10a, b). Lower part of the Hudson River Group, 300-350 ft above low water, Cincinnati, Ohio, U.S.A.

Eocoelia hemispherica crassa Rozman, 1970 (pp. 123-125, pl. 15, figs. 5-8). Upper Ordovician, lower beds of Taskansk Suite, Sette-Daban range, North-east U.S.S.R.

Zygospira resupinata Wang, 1949 (pp. 18-19, pl. 10A, figs. 1-12). *Cornulites* Zone, Brainard Member, Maquoketa Formation (Ashgill), Fairfield, Iowa, U.S.A.

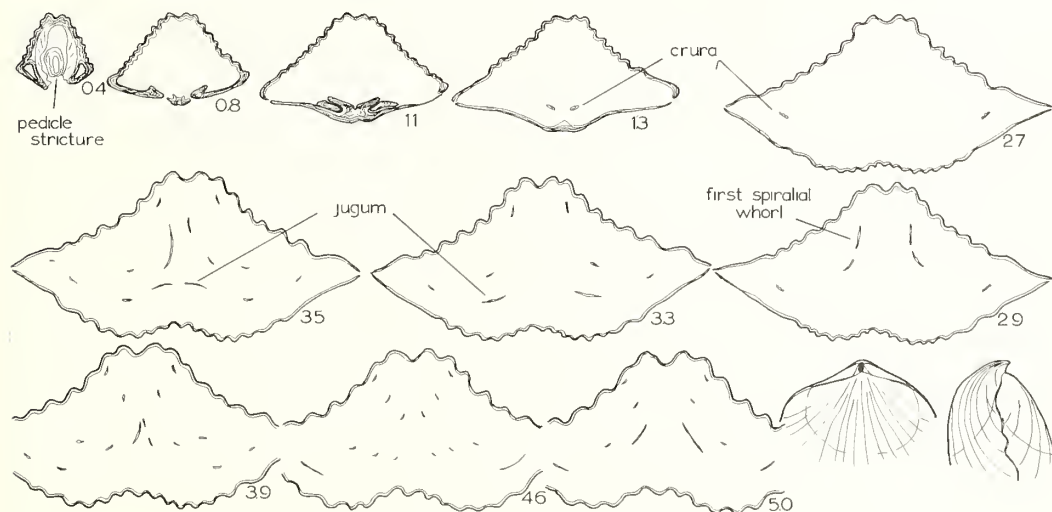
Comparisons. *Zygospira* is distinguished from *Anazyga*, its forerunner, by generally more coarsely ribbed, more strongly carinate shell, differentiated mid and lateral ribs and more planoconvex-ventribiconvex shells. Internally there are more whorls in the adult spiralia and the jugum is located postero-dorsally. Hall and Clarke (1893, p. 154) note an absence of 'dental lamellae', but this is clearly incorrect; dental cavities are prominent in both genera.

Zygospira modesta (Say in Hall, 1847)

Plate 37, figs. 1-8; text-figs. 3-4

1847 *Atrypa modesta* Say in Hall, pp. 141-142, pl. 33, fig. 15.

Type. Lectotype AMNH 1356A (selected by Foerste 1910), Plate 37, figs. 1-4, American Museum Nat. Hist., New York. In the original description Hall noted (1847, p. 142) that the species was rare in New York, where late Ordovician sediments are more sparsely fossiliferous, but abundant in Ohio, Indiana, and Kentucky. He selected no type locality except to state 'It is quite abundant at numerous western localities, particularly Oxford and Cincinnati (Ohio), Madison (Indiana), Frankfort and Maysville (Kentucky)'. When he established the genus in 1862, and also in commenting on the species *modesta* in 1857, Hall cited no source localities. The type specimen is labelled 'Cincinnati'. Foerste (1910, pp. 29-30) examined the type specimen, and stated that although it was labelled 'Cincinnati', this could have meant derivation of the specimen from some Cincinnati collection. The type specimen was labelled 'Hudson River Group'. Foerste (1910) observed that specimens similar to the type came from the Fairmount Bed of the Maysville Formation (late Caradoc) and selected that as the type horizon. Since *Z. kentuckiensis* (Meek) occurs in the Upper Fairmount (according to Foerste), *modesta* may belong to the lower, unless the two taxa were synchronous and allopatric. There is no new data on this, particularly since *Z. modesta* has been very broadly interpreted in the literature and seems to have been ubiquitous in the shallower platform carbonate sequence. Richards (1972) reported *Z. modesta* from the Richmondian Tanner's Creek Formation, well above the typical horizon, but these specimens are not similar to the type material. I have not collected topotype or conspecific material from the Cincinnati region, but judging from other



TEXT-FIG. 4. Serial sections of *Zygospira modesta* (Say in Hall 1847) based on acetate peels. GS 45391 'Cincinnati, Ohio' (material provided by Dr. G. A. Cooper, U.S. National Museum). Scale = 5.

Zygospira in Ontario, abundant in the Georgian Bay Formation, the typical association of *Z. modesta* is with shallow-water benthos, especially digitate bryozoans. Sediments ranged from clayey shales in sub- or peri-biostromal occurrences to finely comminuted bioclastic substrates.

Diagnosis. Moderately sized, wider than long, planoconvex-weakly biconvex zygospirids with 15-18 ribs over all, 4 strong mid-ribs on the pedicle valve, and 3 corresponding mid-ribs on the brachial valve and the remaining lateral ribs decreasing in size posteriorly. Average width 8.1 mm, length 7.2 mm, depth 3.9 mm (based on 15 syntypes in the AMNH Hall Collection). Internally, shell thin; weak, irregular pedicle collar structures line pedicle cavity; dental cavities distinct; teeth near 'horizontal' in sockets (text-fig. 4). Small nodular crural bases on inner socket ridges, crura diverge widely to sides, jugum arising at or near position of cone axes, initially curving postero-medially dorsal to the spiralia, then straightening medially and curving dorso-anteriorly to fuse. Spiralia D-shaped with straight sides forming a weak V (open anteriorly); three to five whorls seen (text-fig. 3). No cardinal process observed; dorsal septum strong. Muscle scars weakly impressed, poorly known.

Remarks. It is premature, without mass collecting, to differentiate clearly between the described species of *Zygospira*, and to delineate an evolutionary succession, but the species group could become a useful tool in zoning late Caradoc-early Ashgill shallow marine sediments. The coarser-ribbed, larger specimens appear to be youngest, but this is not an invariable rule. Some species, such as *Z. kentuckiensis*, show confusing and greater infra-specific variability than do most atrypoids in younger rocks. Most of the described species are from the marine platform carbonate succession of Ontario, Michigan, Ohio, Indiana, and Kentucky. On the Appalachian side and in Quebec, *Zygospira* is rare, and where reported is usually not *Zygospira* but *Anazyga* or *Catazyga*.

Genus ANAZYGA Davidson, 1882

Type species. *Atrypa recurvirostra* Hall, 1847, p. 140.

Range. Caradoc to ?Ashgill. Most if not all 'Trenton' species belong here. This genus is the earliest known wholly ribbed atrypoid. The oldest species appears to be *Anazyga matutina* (Cooper 1956) from the Little Oak Formation, Alabama, whereas the youngest may overlap with *Zygospira* in the late Caradoc to early Ashgill.

Distribution. Most of the species have been identified from eastern North America; also Britain, Scandinavia, and Estonia.

Diagnosis. Small, about 5 mm wide, ventribiconvex-biconvex, equidimensional to elongate zygospirid shells, usually with strongly incurved, anacline-hypercline beaks, fine ribbing, and weak fold-sulcus. Carination lacking. Internally, small dental cavities, minute deltidial plates, undifferentiated teeth. Crura not strongly diverging, jugum branching off anterior to spiralia apices, frequently at the distal side of the crura, then fused postero-dorsally in front of spiralia apices; one to three whorls (text-fig. 5).

Comparisons. *Anazyga* is a widespread genus present in 'Chazy' rocks (Cooper 1956) of Caradoc age in North America (the oldest is in 'Porterfield' equivalents). The most comparable genus is *Hallina* Winchell and Schuchert 1892 whose vertical

range is almost the same. It is possible that *Hallina* is a junior synonym: its type species must be recollected and internal structures clarified. Winchell and Schuchert (1892, 1893) described and figured the brachidia as consisting of a single fused loop, which looks very much like the jugum, but no spiral whorls were noted. If this is typical of all *Hallina*, then possibly the genus is distinct from *Anazyga*. Hall and Clarke (1893, p. 151, figs. 139–141) appear to confirm the lack of a spirulum and presence of a loop, and believed that the internal structure of their genus *Protozyga* (ibid., p. 151) was nearly identical, except that *Protozyga* had the beginnings of the first spiral whorl (ibid., p. 149). If *Hallina* is distinctive in its primitive non-coiled brachidia, then externally it is a near homoeomorph of *Anazyga*, according to Boucot *et al.* (1965). This would create severe taxonomic difficulties in classifying poorly preserved material and would mean that some taxa may be erroneously attributed. Cooper (1956, pl. 143) illustrated *H. saffordi*, *H. lirata*, and *H. globularis*, which indicate that externally *Hallina* may be distinct in having the posterior shell umbones smooth, as already pointed out by Winchell and Schuchert (1893, p. 473). It is possible that the Clintonellinae (Poulsen 1943) may have arisen independently from the *Hallina* group. *Hallina* cannot be distinguished from *Anazyga* by its 'dental plates', which are present in both genera.

Davidson (1883, p. 136) established the family Anazygidae, including *Anazyga*, *Dayia*, and *Hindella*, to include brachiopods with 'loops arising from bottom of spirals'. This was published in the same year as Waagen (1883), who erected the Zygospiridae: thus seniority is not clear. The Anazygidae are left as a junior synonym of the Zygospiridae. Davidson's view was based on a misinterpretation of the coiling direction of the spiralia; the last two named genera have athyridoid spiralia directed at mirror-image position compared to the atrypoids.

Species tentatively assigned.

Atrypa deflecta Hall, 1847 (p. 140, pl. 33, fig. 4a, b). 'Central part of the Trenton Limestone near Martinsburgh.'

Zygospira recurvirostris noquettensis Hussey, 1926 (pp. 162–163, pl. 11, figs. 1–3). Stonington Beds, Ogontz member, Stratton's Farm, northern Michigan, U.S.A. Possibly an unusual *Zygospira*.

Zygospira recurvirostris turgida Foerste, 1917 (p. 103, pl. 5, fig. 15a–c). 'Upper part of the argillaceous Richmond', Little Bay de Noquette, northern Michigan. This may not be true *Anazyga*.

Zygospira orbis Reed, 1917 (pp. 944–945, pl. 24, figs. 24–27). Stinchar Limestone Group, Craighead, Girvan, Scotland (Lower–Middle Caradoc). Possibly a rhynchonellid.

Zygospira variabilis Fenton and Fenton, 1924 (pp. 75–76, pl. 2, figs. 7–9). No single locality cited in literature: Plattin–South Becket Hill, Kentucky; Black River–Frankfort and Paris, Kentucky, U.S.A.

Zygospira variabilis fountainensis Fenton and Fenton, 1924 (p. 76, pl. 2, figs. 1–3). Decorah Shale, Fountain, Minnesota, U.S.A.

Zygospira calhounensis Fenton and Fenton, 1924 (pp. 76–77, pl. 2, figs. 4–6). No locality and horizon in literature.

Zygospira tantilla Bradley, 1921 (p. 525, no figs. but see Pl. 38, fig. 4). Lower Maquoketa, Clermont, Iowa, U.S.A. This is one of the last *Anazyga*, unless a diminutive, unusual *Zygospira* (the type specimens from Harvard University show an orthocline beak, Pl. 37, figs. 16–20).

Zygospira gutta Oraspyld, 1956 (pp. 64–65, pl. 4, figs. 14–15). Vazalemmask Horizon (D_{III}), Saku, Estonia, U.S.S.R.

Zygospira circularis Cooper, 1956 (p. 670, pl. 141C, figs. 18–21; pl. 142B, figs. 6–10; pl. 142D, fig. 16). Upper Carters Formation, Franklin, Tennessee, U.S.A.

Zygospira elongata Cooper, 1956 (pp. 670–671, pl. 268G, figs. 29–32). Lebanon Formation, Readyville, Tennessee, U.S.A.

Zygospira lebanonensis Cooper, 1956 (pp. 671–672, pl. 142C, figs. 11–15). Lebanon Formation, Shelbyville, Tennessee, U.S.A.

Zygospira matutina Cooper, 1956 (p. 672, pl. 141B, figs. 13–17). Little Oak Formation, Alabama, U.S.A.

Zygospira mediocostellata Cooper, 1956 (pp. 672–673, pl. 143D, figs. 13–18). Sevier Formation, Bulls Gap, Tennessee, U.S.A.

Zygospira recurvirostris aequivalvis Twenhofel, 1928 (p. 214, pl. 19, figs. 10–12). English Head Formation, Zone 4, Anticosti Island, Quebec, Canada. Needs confirmation; possibly related to *noquettensis* Hussey, 1926 and *tantilla* Bradley, 1921.

Anazyga recurvirostra (Hall, 1847)

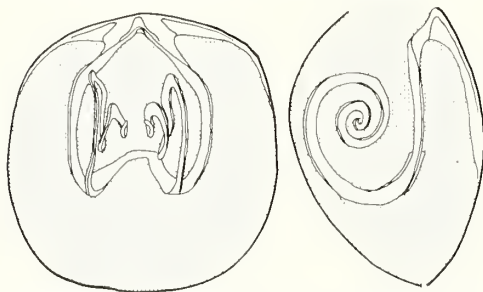
Plate 37, figs. 11–15; text-figs. 5–6

1847 *Atrypa recurvirostra* Hall, p. 140, pl. 33, fig. 5a–d.

Holotype. AMNH 705.3 (by monotypy), Plate 37, figs. 11–15. American Museum Nat. Hist., New York, from 'near Martinsburgh', New York (Hall 1847, p. 140). The species is abundant in thin-bedded, dark-grey argillaceous limestones (micrites), at outcrops just south of the bridge over Roaring Brook, 1.3 miles east of Martinsburg. This seems suitable as a restricted type locality. The type horizon is a 'Compact greyish blue bed of limestone near the centre of the Trenton Limestone' (ibid.: note that this is almost exactly the middle of the Trenton Group on geological maps, e.g. Miller 1910). This horizon is suspected to be the Shoreham Member of the Sherman Falls Formation, or in other terminology, the Sugar River Limestone (Kay 1938), the zone of *Cryptolithus tessellatus* in New York. The Ontario lithic equivalent is the basal Verulam Formation. Clarke (1919), who described the Martinsburg section, listed '*Zygospira recurvirostris*' at the 100, 165–180, 270–280, and 390 ft levels in the Trenton Limestone. It is not known where the type locality of *recurvirostra* mentioned above fits into this sequence.

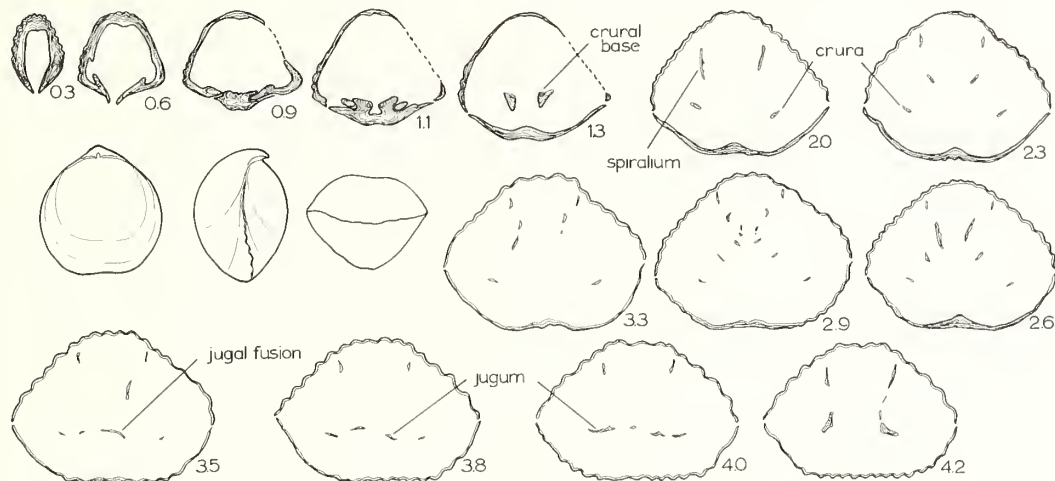
Possibly it is the member 6 of Miller (1910, p. 29) in the Trenton Limestone, said to be 475 ft thick at Roaring Brook, or the 165–180 ft level of Clarke (1919, p. 7). The associated fauna is common hemispherical *Prasopora* colonies, some 2–4 cm in diameter. *Prasopora* tends to be more abundant in the lower middle part of the old Trenton and stops at 280 ft above the base according to Clarke (1919). Other fossils are rare.

Description. Small, 5–7 mm wide, longer than wide, strongly biconvex–ventribiconvex shells with hypercline beaks. Ribs fine, evenly sized throughout, though slightly larger flanking by sulcus, averaging about twenty-four in number. Brachial valve somewhat flattened anteriorly and very faintly sulcate, pedicle valve more arched; weak anterior fold. Internally, pedicle valve thickened apically with faint median septum, no pedicle constrictions, deltidial plates minute, solid, pointed dorsally, dental cavities elongate, teeth simple, dorso-median projections supported terminally by dorsal wall (text-fig. 6). Brachial valve with sturdy, short socket plates separated medially by pit without cardinal process. Crura extended from small round bases located on inner side of socket plates, diverging laterally at about a 45° angle to the mid-shell, then curving inwardly, with spiral whorls beginning at anterior-most portion. Jugum in broad V-shaped band joined anterior to spiralia apex; two to three spiral whorls with axes directed medially (text-fig. 5).



TEXT-FIG. 5. Reconstruction of the spiralia and jugum in *Anazyga recurvirostra*, based on serial sections shown in text-fig. 6. Scale approx. $\times 7$.

Comparisons. It is difficult to compare *A. recurvirostra* adequately with the many other species described later (see list). With its rotund, longer-than-wide shell it seems distinct from other species, but the latter still need revision to determine variation. At the type locality *recurvirostra* is quite consistent in shape and small size, but Hall described the species *deflecta* from what may be the same locality. The type specimens of *deflecta* are lost. Many authors have confused *Z. modesta* with *A. recurvirostra*—the former occurs in much higher strata. In general, *Protozyga* characterizes Blackriveran or older Caradoc beds, *Anazyga* the Trentonian, and *Zygospira* the post-Trentonian. Bretsky (1970) suggested that *recurvirostra* had a



TEXT-FIG. 6. Serial sections of *Anazyga recurvirostra* (Hall, 1847), based on acetate peels. GS 45383, Shoreham Member, Sherman Falls Formation (Trenton Lst.), Roaring Brook, 1.3 miles east of Martinsburgh. Inset are umbonal views. Scale $\times 5$.

functional pedicle, but this seems unlikely in adult stages, which have hypercline beaks developed. He also suggested that the species, which he interpreted more broadly than here, was most common in Virginia and north-west Tennessee. However, it is locally abundant in New York and Ontario (Manitoulin Island area). In Ontario similar species occur in the Bobcaygeon, Verulam, and Lindsay Formations. A statistical comparison of rich material may reveal useful horizon indicators or possibly other geographical or ecological species or sub-species.

Genus *ZYGATRYPA* gen. nov.

Type species. *Zygospira paupera* Billings, 1866, p. 46 (first illustrations, Twenhofel 1928, pl. 21, figs. 21-22).

Range. Llandovery (especially late Llandovery). It must occur in earlier Llandovery strata if derived from *Zygospira*. Upper limit possibly Wenlock.

Distribution. Eastern North America.

Diagnosis. Small, carinate, ventribiconvex-planioconvex zygospirid shells. Fine, usually consistently sized ribs, postero-lateral shell flanks smooth. Minute pedicle

opening, anacline-hypercline beaks, small interarea, and deltidial plates. Commissure sulcate. Internally, valves thick-shelled near hinge and under muscle scars, pedicle constrictures, minute posterior dental cavity or dental nucleus expanded anteriorly to strong teeth. Sockets in brachial valve firm, crural bases elongate, ventro-vertically directed, then sharply laterally turned. Spiralia three to four whorls, dorso-medially directed. Jugum simple, U-shaped, arising posteriorly and joining posterior to spiral apices (text-fig. 7).

Species assigned.

Rhynchonella mica Billings, 1866 (p. 445, no figs.). Jupiter Formation, Zone 9 (Upper Llandovery), Anticosti Island, Quebec, Canada (Twenhofel 1928, pl. 21, figs. 21–22). Plate 37, fig. 30.

?*Atrypa plicatula* Hall, 1843 (p. 71, fig. 4, see also Hall 1852, p. 74, pl. 23, fig. 9a–h). 'Calcareous Shale at Reynale's basin, New York', U.S.A. (Hall *ibid.*). Requires revision.

?*Zygospira minima* Hall, 1879 (p. 14, see Hall 1882, p. 305, pl. 27, fig. 7). Waldron Shale (Wenlock), Waldron, Indiana, U.S.A. If the assignment is correct, this would be the youngest *Zygatrypa*.

Comparisons. *Zygatrypa* is distinguished externally from *Zygospira*, its closest relative, by its finer, even ribbing and its absence of ribs near the hinge line. Internally it is distinct by its more massive teeth, smaller dental cavities or nuclei, thickening sub-muscle field shell wall, crura emergent from the tips of socket plates (as compared with medially in *Zygospira*), but especially by the nature of the spiralia and jugum. The jugum of *Zygatrypa* is U-shaped, whereas in the older *Zygospira*, it is W-shaped (compare text-figs. 3 and 5). In *Zygatrypa* the jugum appears near the hinge line and in *Zygospira* it appears at mid-shell (Beecher and Schuchert 1893).

The Asiatic, later Silurian genus *Tuvaella* is much larger in size, has a long, straight hinge, prominent cardinal process, and lacks dental cavities. The new genus *Zygatrypa* spans part of the stratigraphical gap between youngest *Zygospira* and oldest *Tuvaella*

EXPLANATION OF PLATE 37

All figures $\times 2$, except fig. 21, $\times 4$.

Figs. 1–8. *Zygospira modesta* (Say in Hall 1847). 1–4, AMNH 1356a lectotype, ventral, dorsal, lateral, and posterior views. 5–8, AMNH 1356c paralectotype, ventral, dorsal, lateral, posterior views. 'Hudson River Group, Cincinnati, Ohio', U.S.A. (data on labels of fifteen syntypes). Ashgill.

Figs. 9–10. *Zygospira richmondensis* Caley, 1936. ROM 12448, holotype, ventral and dorsal views. 'Kagawong Fm. Richmond[ian], High Falls, Manitoulin I.', Canada. Ashgill.

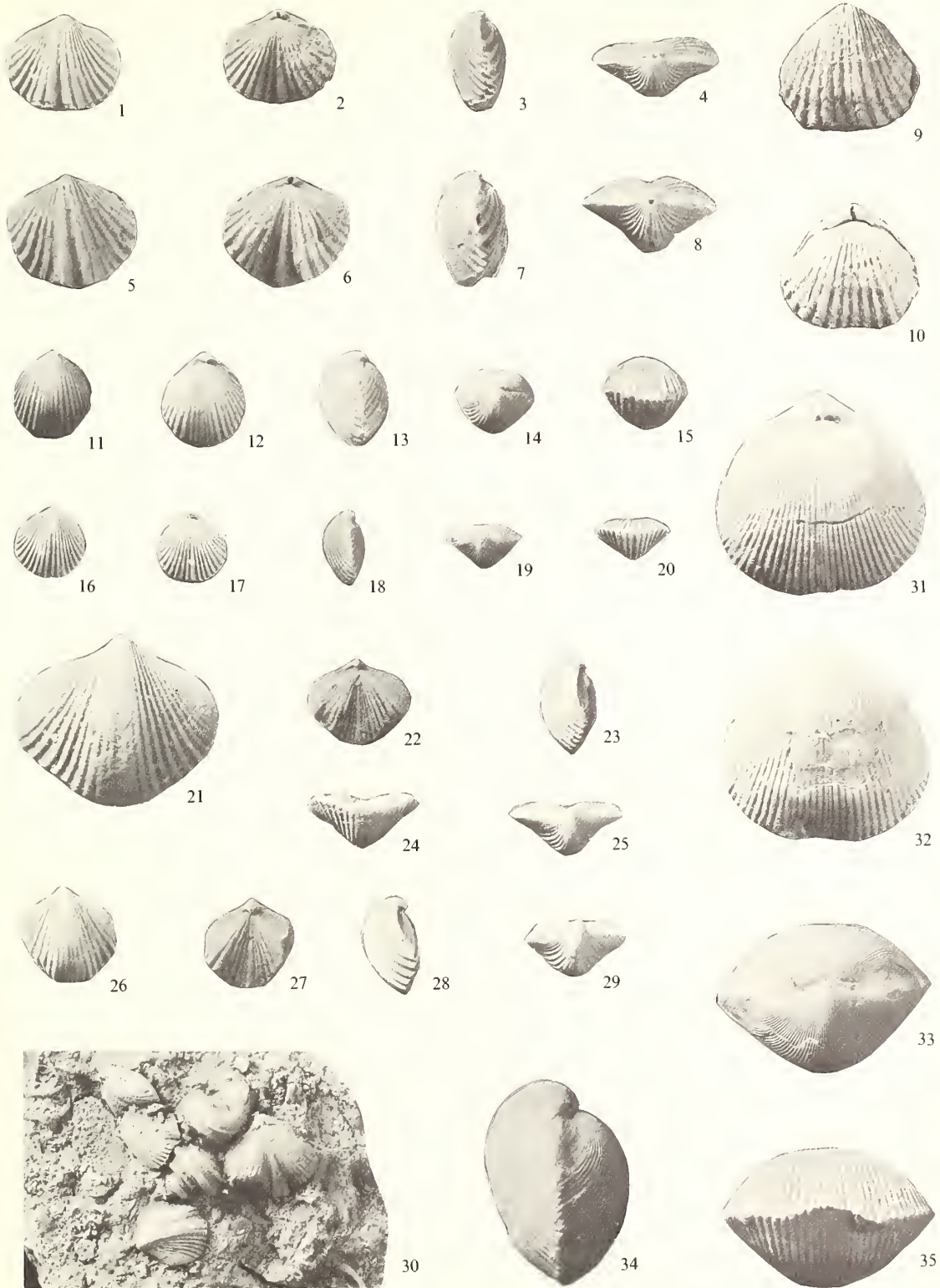
Figs. 11–15. *Anazyga recurvirostra* (Hall, 1847). AMNH 705.3 holotype, ventral, dorsal, lateral, posterior, and anterior views. 'Trenton Lst., Martinsburgh, New York', U.S.A. Caradoc.

Figs. 16–20. ?*Anazyga tantilla* (Bradley, 1921). MCZ8547a lectotype (one of twelve syntypes), ventral, dorsal, lateral, posterior, and anterior views. 'Lower Maquoketa, Clermont, Iowa', U.S.A. Ashgill.

Figs. 21–29. *Zygatrypa paupera* (Billings, 1866). 21–25, GS 2454a lectotype, ventral (enlarged $\times 4$), dorsal, lateral, anterior, and posterior views. Note carination and rib absence postero-laterally. 26–29, GB 2454b paralectotype, ventral, dorsal, lateral, and posterior views. Jupiter Formation (zones 6–7, Twenhofel 1928), Anticosti Island, Canada. Llandovery (top).

Fig. 30. *Zygatrypa mica* (Billings, 1866). GS 2517a, lectotype (largest specimen) and three other syntypes on small slab. Jupiter Formation (Zone 9, topmost), Anticosti Island. Llandovery. Distinguished from older *Z. paupera* by double fold in brachial valve sulcus.

Figs. 31–35. *Catazyga headi headi* (Billings, 1862). Lectotype from Whiteaves Collection, RM 801a, dorsal, ventral, posterior, lateral, and anterior views of the best preserved of four syntypes. 'Trois Rivières, Quebec' (probably Pontgravé River Formation. Ashgill).



COPPER, Ordovician and Silurian Zygospiridae

and was possibly a transitional species group. In particular the jugum of *Zygatrypa* is more like that of *Tuvaella*. Boucot and Johnson (1967) suggested that *Zygospira paupera* may have been ancestral to *Coelospira* (a dayiacean), but this was based on material from California, not Anticosti, and is clearly incorrect. Dayiacean spiralia are like those of the athyridids.

Zygatrypa paupera (Billings, 1866)

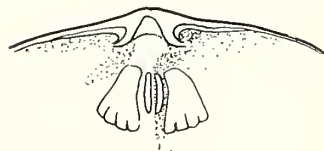
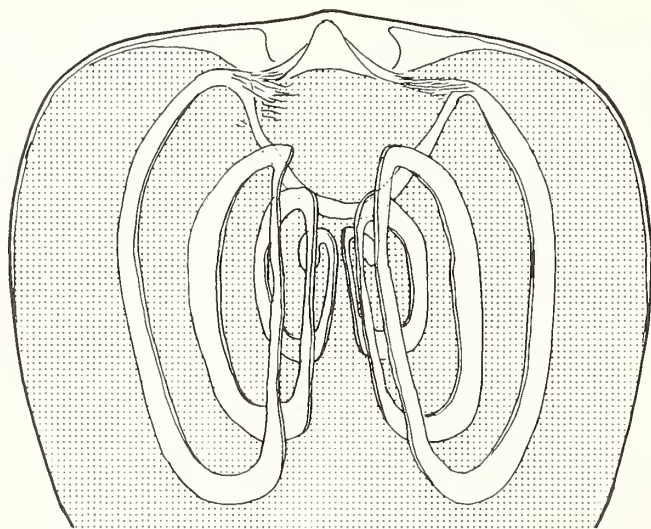
Plate 37, figs. 21–29; text-figs. 7–8

1866 *Zygospira paupera* Billings, p. 46 (Lectotype GS 2454a).

1928 *Zygospira paupera* Billings; Twenhofel, p. 214, pl. 21, figs. 18–20.

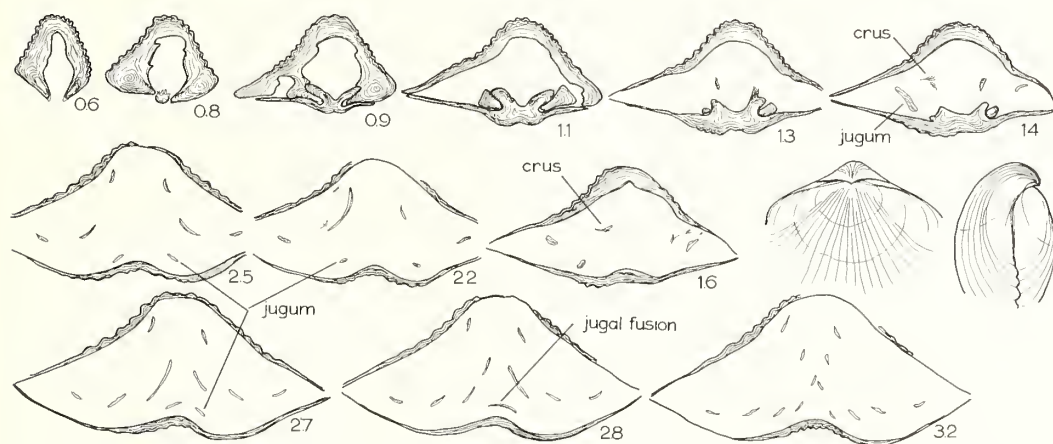
Type locality. 'Near Jupiter River' (Billings 1866), Anticosti Island, Quebec, Canada. From this it seems that the Richardson Collection, on which Billings founded the species, was not actually on the river but close to it. I have been unable to find it in outcrops along the Jupiter, but it was common on the road east of the Jupiter, at firetower no. 5 (NTS 12E/11W, 75180:87940). The type horizon is 'Div. 3, A. G. J. Richardson' (ibid.). This is the Jupiter Formation. Twenhofel (1928, p. 214) remarked that he found the species in Zones 1, 6, 7, and 9 of the Jupiter Formation (Upper Llandoverly), but it probably does not occur in the uppermost zones (8–9), where it is replaced by *Zygatrypa mica* (Billings 1866). I have not seen it in the basal zones of the Jupiter Formation. This leaves zones 6 and 7 as the restricted type strata. The lectotype is one of two syntypes in the Geological Survey (Canada) collections, selected by Twenhofel. GB2454a is the larger and better preserved of these two. The genus occurs in what is probably the equivalent of the *Stricklandia* community, since this pentamerid is abundant in the same few metres of strata. However, *Stricklandia* occurs here in nests, and where it is abundant, *Zygatrypa* is very rare. Instead, *Zygatrypa* occurs in more muddy, yellowish weathering horizons together with other atrypoids such as '*Gotatrypa*' sp. (most abundant), '*Clintonella*' *anticostiana* (next), and *Atryopsis julia* (least common). Trilobites and ostracods are very common but stromatoporoids, corals, and bryozoans are absent.

Description. Small, 6–10 mm wide (average 7.0 mm), wider than long, nearly plano-convex shells with anacline–hypercline beaks, foramen commonly penetrating umbo.



TEXT-FIG. 7. Reconstruction of the spiralia and jugum in *Zygatrypa paupera* (Billings, 1866) based on text-fig. 8. Small cardinal process not shown. Scale approx. $\times 7$.

Apical angle 105° – 120° , interarea narrow, pedicle valve angular convex to almost carinate, brachial valve with deep sulcus dividing two convex halves. Ribs 20–24 in number, absent postero-laterally, especially on the brachial valve; rib pattern in general reveals thick, rarely bifurcating ventral mid-rib, flanked by 3–4 fine ribs, then 3–4 thick ribs, and 3 very faint ribs fading into smooth shell surface. Muscle scars not deeply incised, but raised above valve floor; triangular ventral adductor pad matched anteriorly by two obscure elongated diductor scars divided by a weak septum. The large brachial lateral adductors are shaped like footprints and flank two narrow, central adductors raised on the median septum (text-fig. 7). In serial sections, the pedicle valve shows small, round dental cavities forming the nucleus of simple, inwardly directed teeth. A small cardinal process caps the hinge plate. Diagonal crura fit into notches on the teeth and feather out to a solid U-shaped jugum and spirillum with about three whorls (text-fig. 8).



TEXT-FIG. 8. Serial sections of *Zygatrypa paupera* (Billings, 1866) based on acetate peels. GS 45374, Zones 6–7, Jupiter Formation, Anticosti Island, Canada (Upper Llandovery); NTS Jupiter River 75140:87850. Inset are umbonal views. Scale $\times 5$.

Remarks. The species can be distinguished from younger *Z. mica*, also described by Billings (1866) from Anticosti Island, by the single, angular crest on the pedicle valve in *paupera* against a double crest in *mica*. *Z. mica* appears to be a very scarce element in the uppermost part of the Jupiter Formation on Anticosti Island. Bolton (1972, pl. 8, figs. 15–17, 20) figured a '*Zygospira* *jupiterensis*' from the underlying Gun River Formation. This species can now be assigned to *Atrypina*, and is not a zygospirid. *Zygatrypa* has not been found in the earlier Llandovery strata on Anticosti Island (Gun River, Becscie Formations).

Subfamily CATAZYGINAE subfam. nov.

The *Catazyga* group of Ordovician–Silurian atrypoids include two genera with first appearances in late Ordovician time (late Caradoc), and a decline in post-Ordovician time to eventual extinction by the close of the Llandovery. Included in

the group are the type genus *Catazyga* and also *Pentlandella*. Excluded are *Alispira* Nikiforova, 1961, *Clintonella* Hall and Clarke, 1893, *Nalivkinia* Bublichenko, 1928, and *Anabaria* Lopushinskaya, 1965. The Catazyginae are defined as small to moderately sized atrypoids with uninterrupted tubular ribs, lack of carination, and weak anterior folds and generally biconvex-ventribiconvex shells with small interareas hidden by incurved swollen beaks. Internally they possess a posteriorly located single jugum, and have a modest set of spiral whorls directed dorso-medially. Crura tend to be solidly supported on thick socket plates. Dental cavities are normally absent, but a hidden or weak ventral septum is present; the catazyginids are unusual in their relatively massive deposits along the pedicle cavity and hinge plate.

Nikiforova (in press) has discovered a large late Ordovician atrypoid in Central Asia (Shakhriomon area) which she believes may be a coarsely ribbed catazyginid. The internal structures are as yet undescribed but material available to me shows an atrypoid with distinctive wide interarea, large foramen, and weak carination that may be a large *Zygospira* or spirigerinid; it is not one of the *Catazyga* group (see Pl. 39, figs. 20-23).

Genus CATAZYGA Hall and Clarke, 1893
[*Orthonomaea* Hall, 1893]

Type species. Athyris headi Billings, 1862, p. 147.

Range. Late Caradoc to Ashgill.

Distribution. North America, western Europe; *Catazyga salairica jacutensis* Rozman, 1968 from the north-east U.S.S.R. may not be *Catazyga*. *C. salairica* Severgina, 1960 needs to be investigated. *C. homeospiroides* Ross and Dutro, 1966 does not superficially resemble known catazygids. *C. rara* Nikiforova has become the type species of the genus *Arabaria* Lopushinskaya, 1965, and is not a catazyginid. Thus the genus is not yet confirmed outside western Europe and North America.

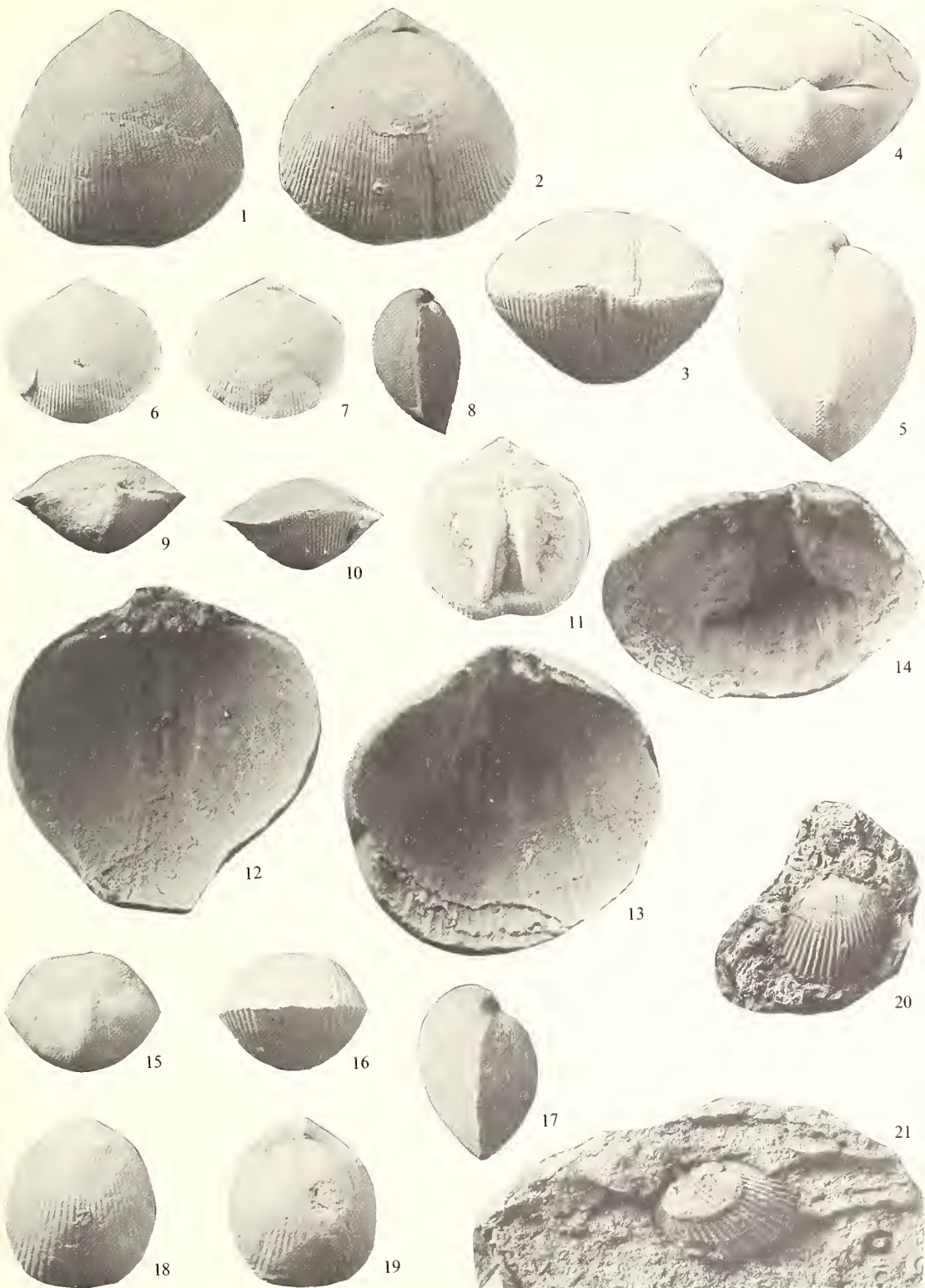
Diagnosis. Small to moderately sized, elongate, finely ribbed, biconvex to ventribiconvex, weakly folded zygospirids with anacline-hypercline beaks covering a minute pedicle opening and deltidial plates (normally not visible). Internally, the

EXPLANATION OF PLATE 38

All figures $\times 2$, except figs. 12-14, $\times 4$.

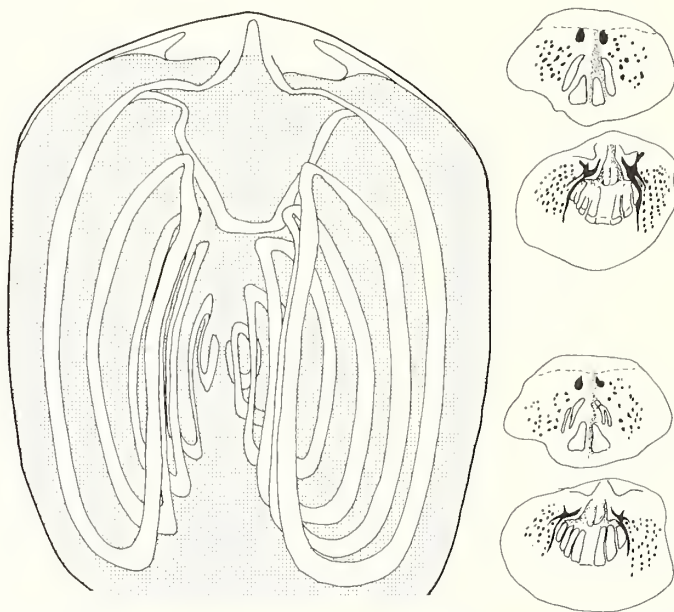
Figs. 1-14. *Catazyga headi headi* (Billings, 1862). 1-5, GS 45385 hypotype, ventral, dorsal, anterior, posterior, and lateral views of large adult specimen with minor growth deformity along sulcus. 6-10, GS 45392 hypotype, ventral, dorsal, lateral, posterior, and anterior views of immature specimen. 11, GS 45401 hypotype, calcined, decorticated mature specimen to show ventral view of the inner spirial whorls. 12, GS 45393, latex mould of brachial valve interior showing muscle field. 13, GS 45391, latex mould of pedicle valve interior. 14, GS 45384, latex mould of pedicle valve interior showing irregularly emplaced muscle field. All material Pontgravé River Formation, Bécancour (restricted type loc.), Quebec, Canada. Ashgill.

Figs. 15-19. *Catazyga anticostiensis* (Billings, 1862). GS 2038j, lectotype (one of fifteen syntypes) from Billings's Collection. Probably from 'Hudson River Fm., English Head, Anticosti I.', and mislabelled in present collection. This material is very similar to other Anticosti material from the Vaureal Formation. Figs. 20-21. *Catazyga hicksi* (Reed, 1905). 20, A30861 paralectotype, internal mould of brachial valve. 21, A30862 lectotype, internal mould of pedicle valve. Cuckoo Grove Lane, Haverfordwest, Wales. Slade and Redhill Formation (Ashgill).



COPPER, Ordovician and Silurian Zygospiridae

pedicle cavity and muscle field is deeply incised and contains thick irregular calcite deposits; small teeth in socket cavities have a massive centrally directed base, dental cavities absent or elongated horizontally. Ventral adductor muscle field broad, subrectangular, divided by weak median ridge; diductor area narrow, tapering posteriorly, poorly defined; dorsal adductors elongate, narrow. Dorsal valve with small cardinal process on thick hinge plates, strong socket plates support small crura. Posteriorly located jugum bent towards cone apices; spiralia three to ten whorls (text-fig. 9).



TEXT-FIG. 9. Reconstruction of the spiralia and jugum in *Catazyga anticostiensis* (Billings, 1862) based on GS 45394, Vaureal Formation; Anticosti Island, Canada, Loc. BF254 MacDonald Rd. Muscle-scar drawings of *C. headi* (Billings, 1862). Approx. $\times 7$.

Species assigned to Catazyga.

Athyris headi borealis, Billings, 1862 (p. 147, fig. 126a-b). 'Hudson River Formation', Lake St. John, on the river Saguenay, Quebec, Canada. *C. borealis* is probably a valid species.

Athyris headi anticostiensis Billings, 1862 (p. 147, fig. 127a-b). Vaureal Formation, English Head, Anticosti Island, Quebec, Canada, Plate 38, figs. 15-19. I consider *C. anticostiensis* a valid species (see Pl. 38, figs. 15-19).

Catazyga headi filistriata Sproule, 1936 (p. 108, pl. 7, figs. 4-7). Upper 30 ft of 'Cobourg strata' (ibid., Lindsay Formation?), Georgian Bay, Ontario, Canada, Plate 39, figs. 1-2.

Zygospira uphami Winchell and Schuchert, 1892 (p. 291, first figs. Winchell and Schuchert, 1895, pl. 34, figs. 45-48). 'Middle of the Galena horizon at Weisbach's Dam near Spring Valley' (ibid., p. 469), Minnesota, U.S.A.

Orthis erratica Hall, 1847 (pp. 288-289, pl. 79, fig. 5a-f). 'Central part of the Hudson River Group' (ibid.), Washingtonville, New York, U.S.A. (Pulaski member of Lorraine, Foerste 1916, p. 37.)

Catazyga uphami australis Foerste, 1909 (pp. 31-32, pl. 2, fig. 19a-b; pl. 3, fig. 14a-c). High Bridge Formation, Camp Nelson member, High Bridge, Kentucky, U.S.A.

Glassia schuchertana Ulrich, 1888 (pp. 186–187, for figs. see Foerste 1909, pp. 32–35, pl. 2, fig. 3; pl. 3, fig. 11a–c). Waynesville Bed (upper part), Hitz Road, Madison, Indiana, U.S.A.

Catazyga cartieri Cooper and Kindle, 1936 (pp. 359–361, pl. 52, figs. 8–13, 18). Whitehead Formation, north-west Percé, Gaspé Peninsula, Quebec, Canada.

Catazyga arcana Williams, 1962 (pp. 247–248, pl. 25, figs. 20–23, 27–28). Kiln Mudstones, Craighead, Girvan, Scotland.

Atrypa headi var. *anglica* Davidson, 1867 (pl. 22, figs. 1–7). Caradoc. Grangegeeth, Ireland.

Species requiring confirmation.

Catazyga homeospiroides Ross and Dutro, 1966 (pp. 8–9, pl. 1, figs. 7, 9–10, 15, 17–20). Thin bedded, shelly limestone unit, Jones Ridge, Charley River, Alaska, U.S.A. Authors state possibility of a distinct genus.

Orthis? sectostriata Ulrich, 1879 (p. 15, pl. 7, figs. 11, 11a–b). Hudson River Group, 300–375 ft above low-water mark in the Ohio River, Cincinnati, Ohio, U.S.A.

Catazyga salairica jacutensis Rozman, 1968 (p. 73, pl. 62, figs. 6–8). Nalchanskaya Suite (late Ordovician), Sakyndani River basin, north-east U.S.S.R.

Catazyga salairica Severgina, 1960. I have been unable to see the original reference.

Zygospira hicksi Reed, 1905 (p. 452, pl. 23, figs. 17–19). Cuckoo Grove Lane, Haverfordwest, Wales, Slade Beds, Ashgillian (A30861–30862, Sedgwick Museum). Plate 38, figs. 20–21.

Comparisons. *Catazyga* is distinguished from Silurian *Pentlandella* externally by its elongate shape, narrower apical angle, and usually larger shells and internally by its muscle field in both valves (raised, arrow-shaped ventral platform in *Pentlandella*), and bulbous socket plates. Some *Catazyga*, but not all, have dental cavities (e.g. the type species has cavities but *C. borealis* (Billings, 1862) does not. The broad-crested, narrow-troughed ribs of *Catazyga* may be a distinct generic feature. For internal distinctions compare text-figs. 9 and 12, 10–11, and 13.

Catazyga headi (Billings, 1862)

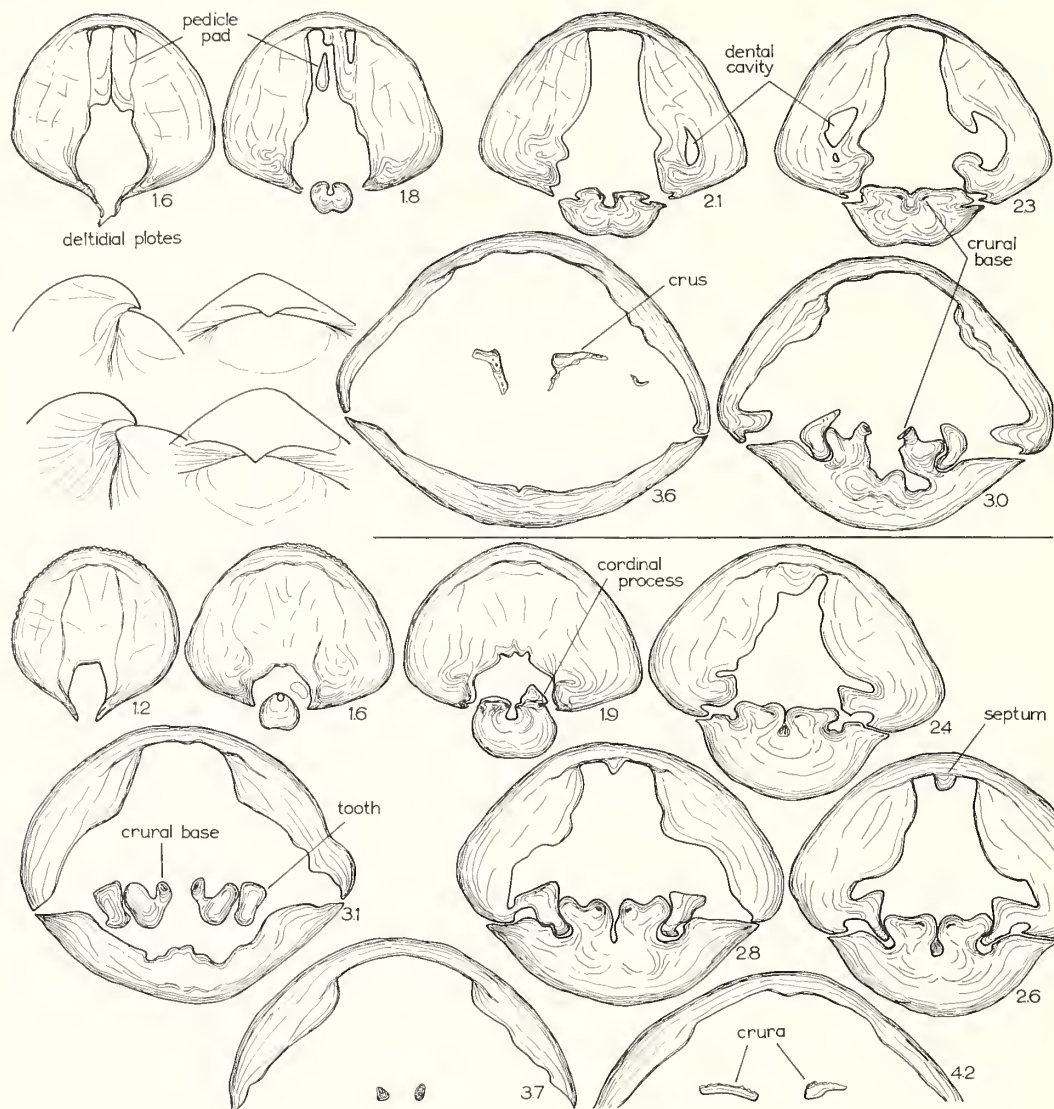
Plate 37, figs. 31–35; Plate 38, figs. 1–14; text-figs. 10–11

1862 *Athyris headi* Billings, p. 147, fig. 125.

Types. Holotype or syntypes lost, at least since the time of Foerste (1909), who mentioned that 'specimens collected by Whiteaves from the type locality are at hand, and may be regarded as replacing the types'. Whiteaves donated four specimens to the Redpath Museum (McGill University, Montreal RM801), which are labelled Trois Rivières, the type locality (Pl. 37, figs. 31–35). None of the four is identical to Billings's figure, which appears to be somewhat larger than life size (width = 19 mm). None of the four is ideal as a neotype, since the exact location of the material is unknown, but Whiteaves probably knew the type locality first hand and therefore RM801a is here selected as neotype. In collections of the Geological Survey, Ottawa, there are fifteen specimens labelled Trois Rivières, collected by J. Richardson in 1856. These specimens are substantially smaller than *C. headi headi* from Trois Rivières and Bécancour and similar in shape and size to *C. anticostiensis* of the Vaureal Formation on Anticosti Island. It is concluded that this suite is mislabelled and represents the lost types of *anticostiensis* described by Billings. The lectotype of the Anticosti species is here selected as GS 2038j, the best preserved of the suite (Pl. 38, figs. 15–19). The type locality is 'On the south shore of the St. Lawrence opposite Three Rivers' (Billings 1862). The exact location of the Billings locality is not possible to trace. Directly opposite Three Rivers at the present time there are no outcrops, only glacial erratics. At the Nicolet River section, some 14 km south of Trois Rivières, the 'gully section' of Foerste (1916, p. 18) probably contains the stratigraphically equivalent horizons (Pontgravé River Formation) with *C. headi headi*, but at present the gully section is not exposed. *C. headi headi* occurs abundantly at Bécancour, about 8 km north of Trois Rivières and a suitable restricted type locality may be NTS Bécancour 3118/W 01450:38880. The type horizon is 'Hudson River formation' (Billings 1862). The Nicolet River section equivalent is probably zones S and T of Foerste

(1916, pp. 18–19) which are in the Pontgravé River Formation ('Richmond'). The Bécancour material is in the same horizon.

Dr. Yvon Globensky, who kindly provided me with a large collection of specimens from Bécancour remarks that the *Catazyga* occur in limestone beds, interstratified with grey, sandy shales. At this locality *C. headi* occurs near the base of the Pontgravé above the Carmel River member. Associated with the atrypoids are solitary rugose corals, *Strophomena* and *Sowerbyella*. The *Catazyga* substrate during life was probably a soft calcareous mud, with specimens orientated beak-down, more due to thicker calcite



TEXT-FIGS. 10–11. Serial sections of two specimens of *Catazyga headi* (Billings, 1862) from Bécancour, Quebec, Canada (near Trois Rivières), NTS Bécancour 01450:38880. Top GS 45398; bottom GS 45397. Note the variation in pedicle deposits, typical of many later atrypoids. External views of the umbonal region are inset. Scale $\times 5$.

deposition in the umbonal region, than to anchoring. Sectioned specimens frequently show muddy infilling posteriorly and vugs or drusy calcite anteriorly.

Diagnosis. Medium sized to large, globose *Catazyga* with maximum width at mid-length, hypercline beaks, foramen and area obscured at maturity. Pedicle valve more convex than brachial valve, often with weak narrow anterior brachial valve sulcus and broad pedicle valve fold (over all weakly uniplicate). Internally distinctive muscle fields, thick pedicle callosities, small outwardly extended deltidial plates, dental cavities horizontally elongated, teeth massive, lacking accessory lobes, cardinal process irregular, bulky; crura thick. Spiralia-jugum unstudied. Spiridium reconstruction based on *C. anticostiensis* (text-fig. 9).

Description (based on Bécancour locality). Shells average width, peaks at 14 mm, maximum 19 mm, depth peaking at 9 mm, mostly longer than wide (text-fig. 6), apical angles 105–110° (average 108°). Pedicle area covered by beak in very early growth stages, before shell is 10 mm wide; sometimes pedicle opening expanded as slit in umbo. Ribs very fine posteriorly (at 5 mm, 25–30 ribs per 5-mm arc) but at 20 mm from umbo coarsening to 8–11 ribs per 5-mm arc; ribs round-broad crested and narrow-troughed. Brachial valve less convex but well-rounded; both valves usually sulcate with the pedicle valve having broad, flat sulcus. The adductor muscle fields are quite variable. The ventral adductor pad occupies about a quarter of the shell length, is wider than long, rectangular to rounded, and frequently skew or irregular; medially it is divided by a broad, low septum and laterally each side has three to four grooved lobes (usually three). The ventral diductors appear to be raised on two rounded irregular lobes, fusing posteriorly and sometimes raised off the shell floor. These structures may represent pedicle muscle callosity, and if that is the case the diductors possibly are located between the pedicle callosity and the adductor field. The dorsal muscle field is difficult to interpret. Adductors are in the form of two pairs, a posterior bean-shaped pair and an antero-medial pear-shaped pair divided by a rounded median septum. Closer to the hinge plate are one to three pairs of small depressions of unknown origin, possibly accessory diductors (text-fig. 9).

The serial sections illustrated (text-figs. 10–11) are largely self-explanatory. Most striking are the thick pedicle cavity linings (squared in outline) and massive hinge plates generally lacking in zygospirinids. The axis of the dental cavity is dorso-anteriorly ventral posteriorly and horizontal anteriorly; teeth are simple stumps, free anteriorly. The pedicle opening is either hidden or sometimes expanded into the ventral umbo as a minute, narrow slit; deltidial plates are pointed dorsally rather than medially. A cardinal process is present in the form of thick irregular outgrowths capping the ends of the socket plate, expanding well into the pedicle cavity; the groove between the socket plates is narrow and slit-like. The crura arise from a point source hidden deep within the hinge plate, and are rounded in cross-section; anteriorly they stand free as thin, raised ridges and then direct themselves ventrally and sharply laterally. Further brachidial structures still unknown (see reconstruction of complete *C. anticostiensis* in text-fig. 9).

Remarks. *C. headi*, like all *Catazyga*, had a small functioning pedicle or loss of pedicle in maturity. Epifauna was very scarce on the shells examined, and where found, consisted of small serpulids (*Cornulites*?) and *Hederella* normally located

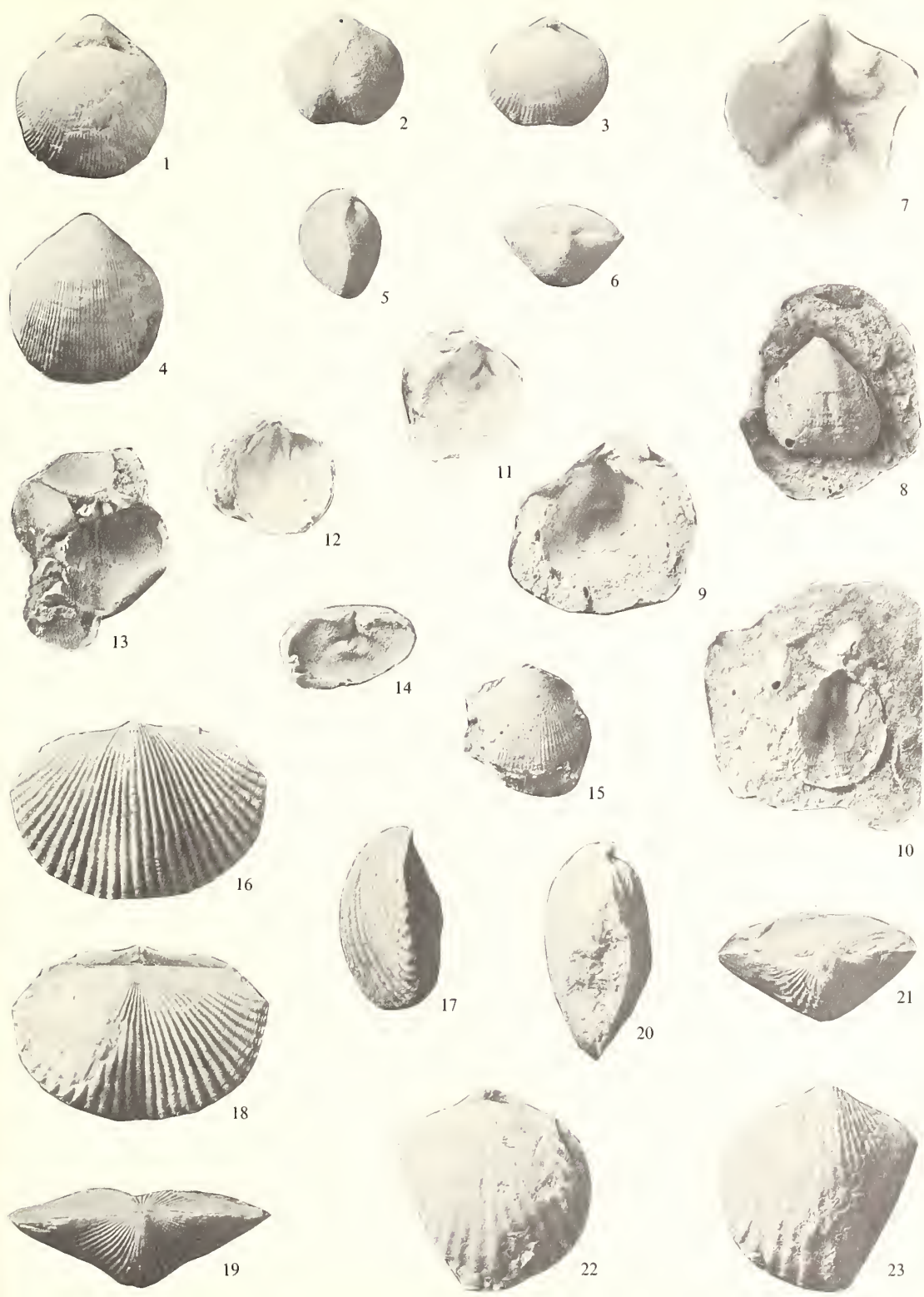
on the anterior central part of the pedicle valve. The probable mode of life of *Catazyga* was with the umbo down and shell vertical or angled with the pedicle valve uppermost, considering the evidence of epifauna, thick shell callosities posteriorly, and the usual posterior mud infilling of the shell after death. Slabs of *C. anticostiensis* which contain large numbers of presumably death-orientated shells show a prevailing umbo-down position; clusters of the same *Catazyga* show orientation towards a common point of fixation, and possibly indicate a thin, thread-like pedicle.

The species of *Catazyga* at present are no more useful as stratigraphic indicators than mentioned by Foerste in 1924 (pp. 129–130). According to Foerste (1916) *C. erratica* precedes *C. headi* in the Quebec–Ontario sequences. In Ontario, *C. filistriata* in turn appears to precede *C. erratica* and possibly the oldest *Catazyga* is *C. uphami* from Minnesota. If this sequence is correct, then no distinctive external trends are present in the *Catazyga* lineage, except possibly increasing size. Shape, convexity, and structure of the anterior commissure were random developments at different times and in different places. Lineages of *Catazyga*, which was a deeper quiet-water inhabitant, are rarely continuous in contiguous sections, and thus reflect water-depth variability and fluctuations in different regions. Such changes will be calculated when more data is available on over-all distribution. *C. headi* is not sufficiently distinct externally from *C. erratica* to warrant the separate genus *Orthonomaea* Hall, 1893 for the latter. The species of *Catazyga* also are not sufficiently well known to split off a new genus on the presence or absence of dental cavities (or ‘dental plates’), as with other Palaeozoic atrypoids.

EXPLANATION OF PLATE 39

All figures $\times 2$, except fig. 7, $\times 4$.

- Figs. 1–2. *Catazyga filistriata* Sproule, 1936. ROM39a lectotype (one of six syntypes), ventral and dorsal views. ‘Upper 30 ft. of Cobourg strata’ (below Collingwood Black Shale). Locality unknown, possibly old quarry at Bowmanville (Sproule 1936, p. 99), Canada. Caradoc.
- Figs. 3–7. *Pentlandella tenuistriata* Rubel, 1970. 3–6, GS 45395 hypotype, ventral, dorsal, lateral, and posterior views of adult specimen. 7, GS 45394, interior view of pedicle valve enlarged ($\times 4$) to show the arrow-shaped muscle field. Latikula, Estonia, U.S.S.R.; Adavere Formation. Upper Llandovery.
- Figs. 8–12. *Pentlandella pentlandica* (Haswell, 1865). 8, BMNH 12630a hypotype, latex mould of external of pedicle valve. 9, BMNH 12730b, hypotype, latex mould, internal view of pedicle valve. 10, BMNH 12730c hypotype, latex mould, internal view of brachial valve. Pentland Hills, Scotland, Bed D, Esk section. Upper Llandovery. 11, BMNH 12632a, latex mould, internal view of pedicle valve. 12, BMNH 12632b, latex mould, internal view of brachial valve. Same horizon and locality.
- Figs. 13–15. *Pentlandella haswelli* (Reed, 1908). 13, A32775b paralectotype, latex mould of internal of brachial valve. 14, A32271 lectotype, latex mould of internal of pedicle valve showing muscle field in hatchet-shape more comparable to *Catazyga*. 15, A32275a paralectotype, latex mould, external of pedicle valve. ‘The Frolic, Haverfordwest’, Dyfed, Wales. Lower Llandovery.
- Figs. 16–19. *Tuvaella rackovskii* Chernyshev, 1937. GS 45393 hypotype, ventral, lateral, dorsal, and posterior views of adult specimen. Elegeist River, Tuva, U.S.S.R. Wenlock. (See Vladimirskaia 1973.)
- Figs. 20–23. Undescribed genus (Nikiforova, in press). GS 45396, hypotype, lateral, posterior, dorsal, and ventral views of adult specimen. Khrebt Shakhriomon, central Asiatic U.S.S.R., Ordovician O₃ (Ashgill). Affinities of this taxon are still unclear—may be ancestral to *Tuvaella*, or possibly a spirigerinid.



COPPER, Ordovician and Silurian Zygospiridae

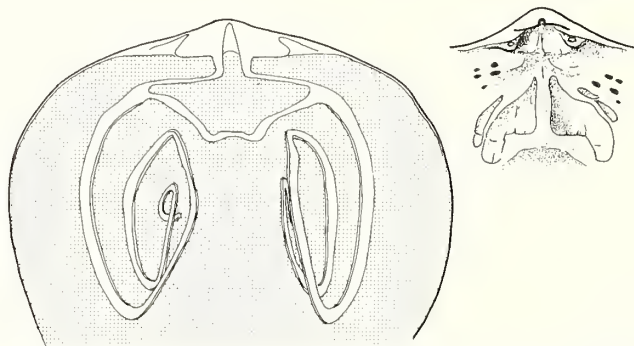
Genus PENTLANDELLA Boucot, 1964

Type species. *Rhynconella pentlandicus* Haswell, 1865 [sic], p. 31, pl. 3, figs. 9-10. (See Pl. 39, figs. 8-12.)

Range. Llandovery.

Distribution. Scotland, Wales, and Estonia.

Diagnosis. Small, globose, ventribiconvex, finely ribbed shells with hypercline beaks, minute foramina, and weak fold-sulcus. Ribs have micro-growth lines but no major interruptions; apically ribs are very faint to absent. Internally, the pedicle valve is thickened posteriorly; the brachial valve is also strong. Groove for ventral adductor and diverging diductors implanted into raised median septum. Dorsal muscle field flabellate, also divided by septum. No dental cavities or nuclei, teeth have wide bases, pointed extremities. Cardinal process apparently absent. Crura bases ball-like, thin crura rapidly spread laterally from crural bases. Jugum posteriorly located, joined almost at first spiral whorl, shaped like flattened W, or U with square corners. Spiralia with three to four whorls medially and medio-dorsally directed (text-fig. 12).



TEXT-FIG. 12. Reconstruction of spiralia and jugum in *Pentlandella tenuistriata* Rubel, 1970, based on text-fig. 13. Approx. $\times 7$.

Species assigned.

In addition to the type species, only two other species appear to be known:

Zygospira haswelli Reed, 1908 (pp. 434-435, pl. 14, figs. 4-9). Haverford Mudstone Formation (Lower Llandovery), 'Locality K, below the path SW. of Uzmaston Farm', Wales (label on lectotype A32771, Sedgwick Museum). Plate 39, figs. 13-15.

Pentlandella tenuistriata Rubel, 1970 (pp. 27-28, pl. 17, figs. 1-24). Adavere Horizon, Estonia, U.S.S.R. (Upper Llandovery), figured by Rosenstein 1941, p. 6, fig. 74a incorrectly as '*Catazyga furcata*' (Sowerby, 1839); the Sowerby species is not atrypoid.

Comparison. *Catazyga* is the most similar atrypoid genus, but differs in its muscle field and septal structures, simpler jugum and larger spiralia, and in its massive, bulbous tissue surrounding the crural bases. As the last-surviving catazyginid, ranging into late Llandovery time, and maybe the Wenlock, *Pentlandella* is not a widespread genus. It appears in Estonia to be a deeper-water inhabitant, like Ordovician *Catazyga*, which may explain its rarity in the Llandovery of Wales and

the Welsh Borderland. The genus is absent in richly fossiliferous Llandovery rocks of Anticosti Island, and those of the Siberian Platform, suggesting a provincial distribution. It is possible that the raised muscle areas of *Pentlandella* represent a trend towards a septally elevated muscle field such as in the mid-Devonian *Gruenewaldtia*. However, there are no connecting taxa, and raised muscle fields were independently developed in other different atrypoid lineages. The older *P. haswelli* has a hatchet-shaped ventral muscle field, becoming arrow-shaped in *P. pentlandica*.

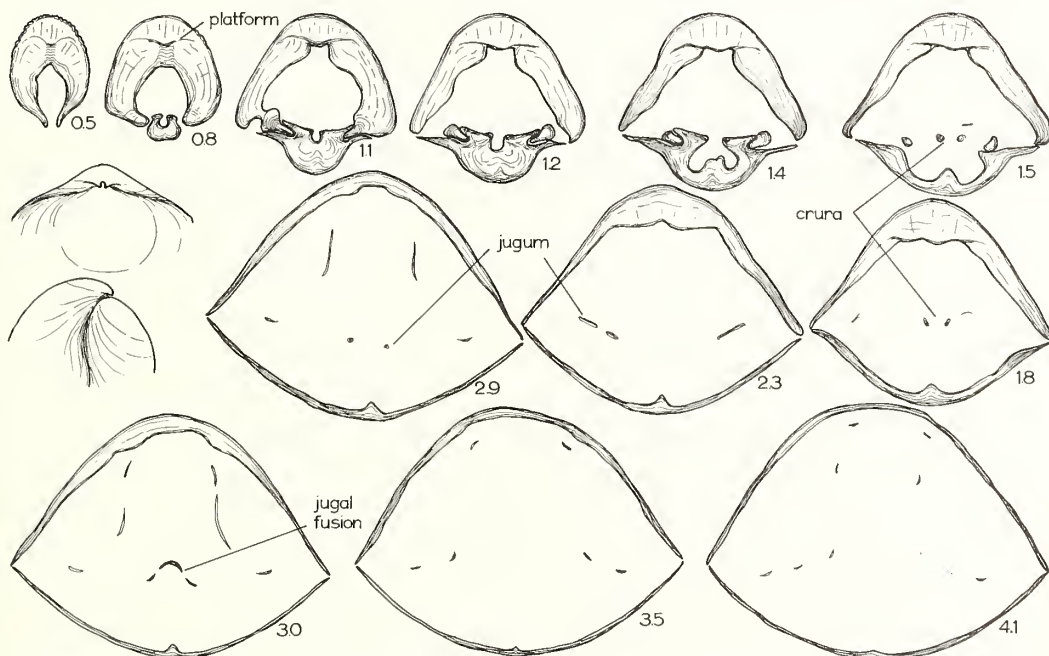
Pentlandella tenuistriata Rubel, 1970

Plate 39, figs. 3-7; text-figs. 12-13

Remarks. Rubel (1970) has well illustrated the external features of the Estonian species. Detailed internal serial sections, however, have not previously been available. Material for sectioning was made available to me by Dr. Rubel. The sections can now be compared adequately with those of *Catazyga* and other zygospirids (text-fig. 13). Note especially the thickened posterior shell wall portions, crura, and spiralia.

Subfamily TUVSELLINAE Alikhova, 1960 (emend.)

Vladimirskaya (1972) pointed out that *Tuvaella* had dorsally directed spiralia and would be more correctly placed in the Zygospiridae amongst the atrypoids, instead



TEXT-FIG. 13. Serial sections of *Pentlandella tenuistriata* Rubel, 1970 based on acetate peels. GS 45381, Adavere Horizon (Upper Llandovery); Latikula, Estonia, U.S.S.R. The type species of *Pentlandella* and related British species are preserved as moulds and unsuitable for sectioning. Scale $\times 5$.

of in the Orthacea. Alikhova (1960) had erected a special family, with a single genus, in the Orthacea to account for its peculiar morphology. Through the kindness of Dr. Vladimirskaia, who presented me with a suite of specimens, I was able to examine well-preserved specimens of *Tuvaella* from Tuva in the Asiatic U.S.S.R. This has led to a slightly revised diagnosis and some new discoveries.

The Tuvaellinae are unique in their stratigraphical distribution in rocks of latest Llandovery through Ludlow age. In addition to their size, and flattened dimensions, making them the largest known zygospirids, the Tuvaellinae are distinctive in several respects: they possess wide, flat interareas, a massive cardinal process and very thick hinge plates, and a dorsal jugum which comes to a blade-like, ventrally directed point between the spiral cones. They also differ from Zygospirinae by their lack of dental cavities or nuclei. They belong clearly to the Zygospiridae on two counts: firstly, their jugum is dorsal to the spiralia (as against ventral in all other atrypoid stocks), and secondly, the jugum is one piece (as opposed to two separated processes; see text-fig. 14). Otherwise, externally *Tuvaella* itself has a strong resemblance to the *Carinatina* group of the Devonian. It may have evolved independently in that direction, but other ancestors for the Carinatinae lie more in the range of *Neospirigerina* Rzhonsnitskaya, 1975.

A possible ancestor to the Tuvaellidae may be an undescribed genus (Nikiforova, in press; see Pl. 39, figs. 20–23) from late Ordovician rocks of central Asia (Shakhriommon area). Poorly preserved material given to me by Dr. Nikiforova reveals a coarsely ribbed, large, weakly carinate, zygospirid shell, possessing a clear, relatively wide shelf-like interarea, large exposed foramen, and deltidial plates and orthocline-anacline beak. However, internal structures are still unknown, and the poorly preserved material may be a *Spirigerina* or *Eospirigerina*. There are probable phylogenetic ties from *Tuvaella* to the Devonian sub-family Carinatinae, including *Biconostrophia* Havlíček, 1956 (and its synonym *Davidsoniatrypa* Lenz, 1968), *Pro davidsonia* Havlíček, 1956, *Davidsonia* Bouchard-Chantereux, 1849, *Carinatina* Nalivkin, 1930, and *Eifelatrypa* Copper, 1973. Some, if not all, of these taxa have highly developed cardinal processes and rather similar hinge plates. If this assumption proves correct, then the Palaferrellidae, in the sense of Struve (1961) and Copper (1973), are polyphyletic, and need restudy.

Genus TUAELLA Chernyshev, 1937

Type species. *Tuvaella rackovskii* Chernyshev, 1937, p. 12.

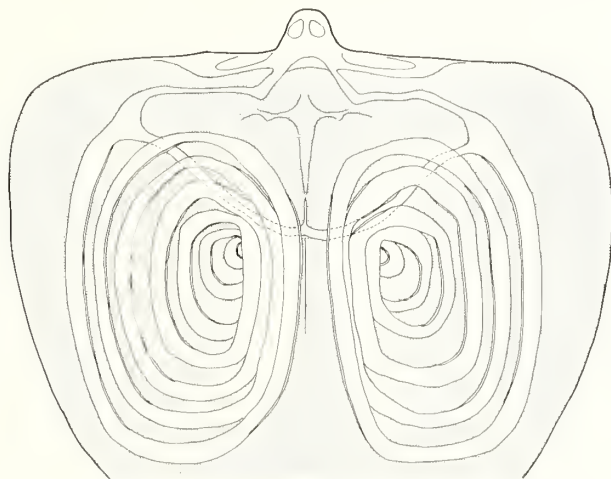
Range. Wenlock–Pridoli(?).

Distribution. Asiatic U.S.S.R., Mongolia.

Diagnosis. Relatively large and wide, coarsely and evenly ribbed zygospirids with somewhat carinate ventral fold and dorsal sulcus. Hinge line long, straight; inter-area wide and extensive; beaks orthocline to partly anacline; foramen covered by thick deltidial plates. Internally solid teeth, a strong cardinal process, dorsally to medio-dorsally directed spiralia, and a jugum arising posteriorly with a central spine-like meeting point are characteristic of at least the type species (internals of other species not known).

Tuvaella rackovskii Chernyshev, 1937

Plate 39, figs. 16–19; text-figs. 14–15

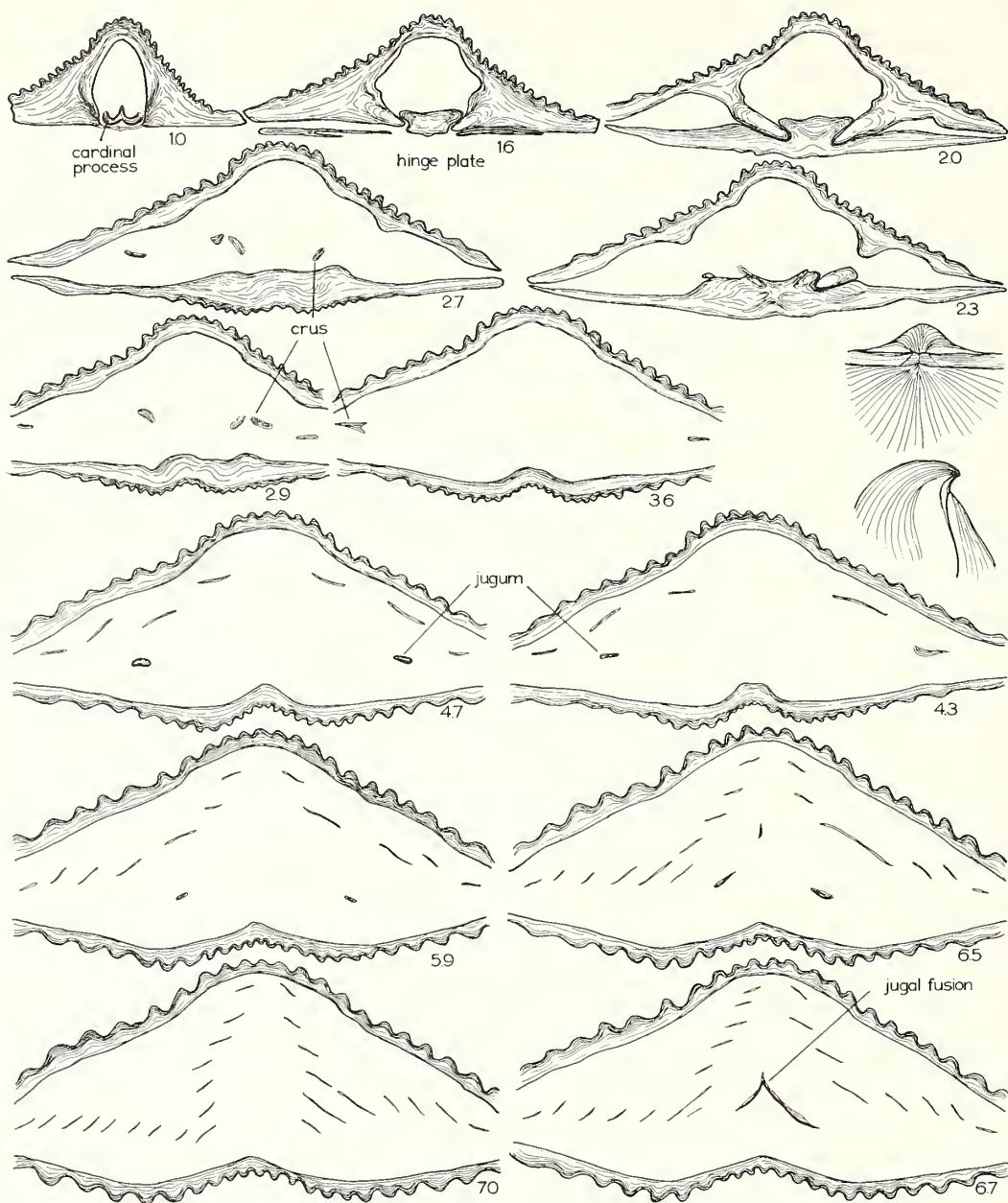
1937 *Tuvaella rackovskii* Chernyshev, pp. 12, 64, pl. 1, figs. 8–11.1972 *Tuvaella rackovskii* Chernyshev; Vladimirskaia, pp. 39–42, pl. 6, figs. 1–14.*Range.* Llandovery–?Wenlock or Ludlow.*Distribution.* Altai Mountains, Tuva, western Sayan, eastern Transbaikal, and north-east U.S.S.R. (Amur region), Mongolia. Not known outside U.S.S.R. and Mongolia.*Remarks.* Vladimirskaia (1972) provided the first detailed internal description of the type species of *Tuvaella*, including serial sections and photographs of the brachidia. Differential, partial recrystallization of the shells permitted Vladimirskaia to etch specimens to bring out specific features. At the same time this recrystallization alsoTEXT-FIG. 14. Reconstruction of the brachidia in *Tuvaella rackovskii* Chernyshev, 1937 based on text-fig. 15.

obscured the original shell and brachidial structure. I was unable to discover the canals in the dorsal median septum in unrecrystallized material: possibly recrystallization of the shell can give the impression of the existence of such canals. The enormous cardinal process, projecting well into the pedicle cavity is unusual. The crura do not geniculate at the angle shown by Vladimirskaia in the material sectioned by me. The jugum is broadly convex and not angular and projects medially into a remarkable blade (text-fig. 15), not known in any other atrypoids. This may have held mouth parts, or less possibly muscle structures.

Family ATRYPIDAE Gill, 1951

Subfamily CLINTONELLINAE Poulsen, 1943

Shells characteristic of this subfamily are biconvex, tubular-ribbed, usually non-carinate, non-lamellose, thin-walled, and with a narrow interarea, small beak, and



TEXT-FIG. 15. Serial sections of *Tuvaella rackovskii* Chernyshev, 1937 based on acetate peels. GS 45377, Wenlock; Elegest River, Tuva, U.S.S.R. Inset shows the pedicle structure. Scale $\times 5$.

small deltidial plates. Internally the group has relatively large dental cavities, thin hinge plates, delicate narrow crura, separated ventrally located jugal processes, and dorsally directed spiralia. This subfamily has characteristics similar to those of Devonian *Desquamatia*. Nikiforova and Modzalevskaya (1968) placed *Nalivkinia* (*Anabaria*), alongside *Alispira*, in the family Atrypidae, without special subfamily designation. Lopushinskaya (1965) assigned it to the Clintonellinae. Kulkov (1967) thought that *Nalivkinia* was related to the Karpinskiinae via *Eokarpinskia* Rzhonsnitskaya, 1964, and later referred it to the Atrypinae (Kulkov 1974). In 1973 I allocated *Nalivkinia* to the Atrypidae (erratum under Zygospiridae, p. 488) and *Alispira* and *Clintonella* to the Zygospiridae. Work on serial section internals convinces me that Lopushinskaya's interpretation is substantially correct, that is the Clintonellinae form a genus group including *Clintonella*, *Alispira*, and *Nalivkinia*. These are still believed to have evolved independently from the main *Atrypa* group as shown in Copper (1973). Because of the lack of brachidial data on the three clintonellinid genera, I am hesitant about suggesting other affinities. Possibly some of the Palaferellidae, like *Gracianella* and *Eokarpinskia*, are related to *Nalivkinia* (*Anabaria*). Alternatively affinities with Devonian *Desquamatia* or *Carinatinella* are suggested in morphology of the dental cavities and brachidia. The Clintonellinids lack the thicker, more massive shells of the palaferellids and their reinforced jugal processes, but may have moved in that direction by changing habitats from quieter marine to the higher-energy reef areas favoured by many palaferellids.

Genus NALIVKINIA Bublichenko, 1927

Type species. *Atrypa grünewaldtiaeformis* Peetz, 1901, pp. 147–148, 376, pl. 4, fig. 2a–c from the Sarachumysk River, Kuznetsk Basin, U.S.S.R.

Range. Upper Llandovery–Wenlock (possibly to the lower Devonian).

Distribution. Tuva, Altai Mountains, Salair, Kazakhstan, Central Asia.

Remarks. *Nalivkinia* ranging from Llandovery to the late Silurian and possibly into lower Devonian time, appears at present to have been found only in the U.S.S.R. Bublichenko (1927) recognized a new genus in the Peetz species and, in addition to the type, described a new species, *N. sibirica*, apparently from the same locality and horizon. Subsequently, Nikiforova and Andreeva (1961) described a species they called *Catazyga rara* from the Siberian platform, later identified by Lopushinskaya (1965) as belonging to a new subgenus *Anabaria* within *Nalivkinia*. Internally the only difference between them lies in the thicker muscle pads in *Nalivkinia* and externally in the greater globosity and beak incurvature. Identical features in the two taxa are the large dental cavities, 'hair-line' structures of the dental plate, and delicate crural bases and crural supports feathering distally. These similarities at present outweigh the differences on a generic level. The two subgenera are maintained because of lack of comparative brachidial evidence. The internal structure of these atrypids is more 'advanced' than the zygospirids and members of the *Atrypa reticularis* group in the presence of clearly definable socket plates, more delicate crura, and a striated cardinal process in the notothyrial pit.

Species assigned to Nalivkinia (Nalivkinia).

Inadequate data exists on the correct assignment of many Silurian atrypoid species referred in the past to *Nalivkinia*, *Gruenewaldtia*, or *Atrypa*. Any number of these could belong to *Nalivkinia (Nalivkinia)*: doubtful species are preceded by a question mark.

Nalivkinia sibirica Bublichenko, 1927 (p. 983, fig. 1; pp. 990–991, pl. 49, figs. 2, 7–8; pl. 50, figs. 4–10). This species occurs together with the Peetz type species in the same strata. It appears to be indistinguishable by its sulcus and more globose shell as described, and may be a population variant.

?*Nalivkinia linguata* Borisyak, 1955 (pp. 65–66, pl. 10, figs. 4–9; pl. 13, figs. 8–10). Llandovery–Wenlock of central Kazakhstan, U.S.S.R.

Nalivkinia minuta Menakova, 1964 (pp. 26–27, pl. 5, figs. 8–10). Daurich Mountains, U.S.S.R., Wenlock, Bed 'L'.

Nalivkinia (Nalivkinia) gruenewaldtiaformis Peetz, 1901

Plate 40, figs. 1–4; text-fig. 16

1901 *Atrypa gruenewaldtiaformis* Peetz, pp. 147–148, 376, pl. 4, fig. 2a–c. Holotype, Leningrad University Museum, specimen 81/90.

1927 *Nalivkinia gruenewaldtiaformis* Peetz; Bublichenko, pp. 989–990, 1002–1003, pl. 50, figs. 1–3.

1967 *Nalivkinia gruenewaldtiaformis* Peetz; Kulkov, pp. 106–108, pl. 18, figs. 1–2.

1974 *Nalivkinia gruenewaldtiaformis* Peetz; Kulkov, pp. 61–62, pl. 21, figs. 3–6.

Remarks. Both Bublichenko (1927) and Kulkov (1974) illustrate a connected jugum for the type species of *Nalivkinia*. However, serial sections in Kulkov (1974, p. 62) indicate that the jugal processes are only very weakly joined together, and possibly recrystallization has obscured what may actually be disconnected structures. This is similar to many reconstructions for Devonian Atrypidae, which have been shown to be incorrect (Copper 1967). Jugal processes frequently come so close together that they are easily confused for being fused. More work is still needed on the interior of *Nalivkinia*. Significant apical internal structures of *N. gruenewaldtiaformis* are the large dental cavities, the presence of a thin true dental plate (appearing as a 'hair-line' structure in serial peels) along the inner margin of the pedicle cavity,

EXPLANATION OF PLATE 40

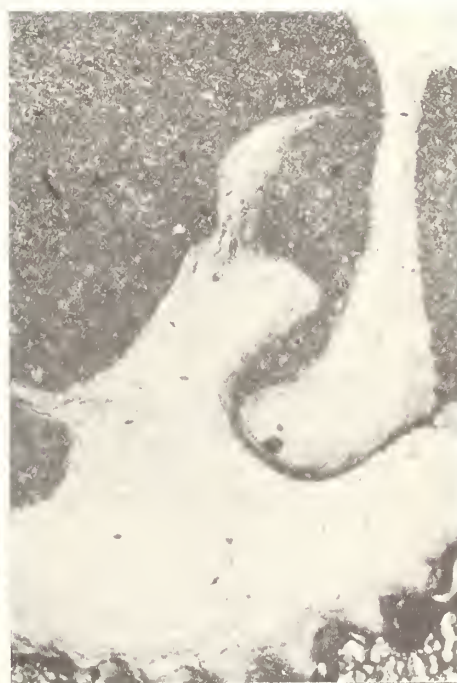
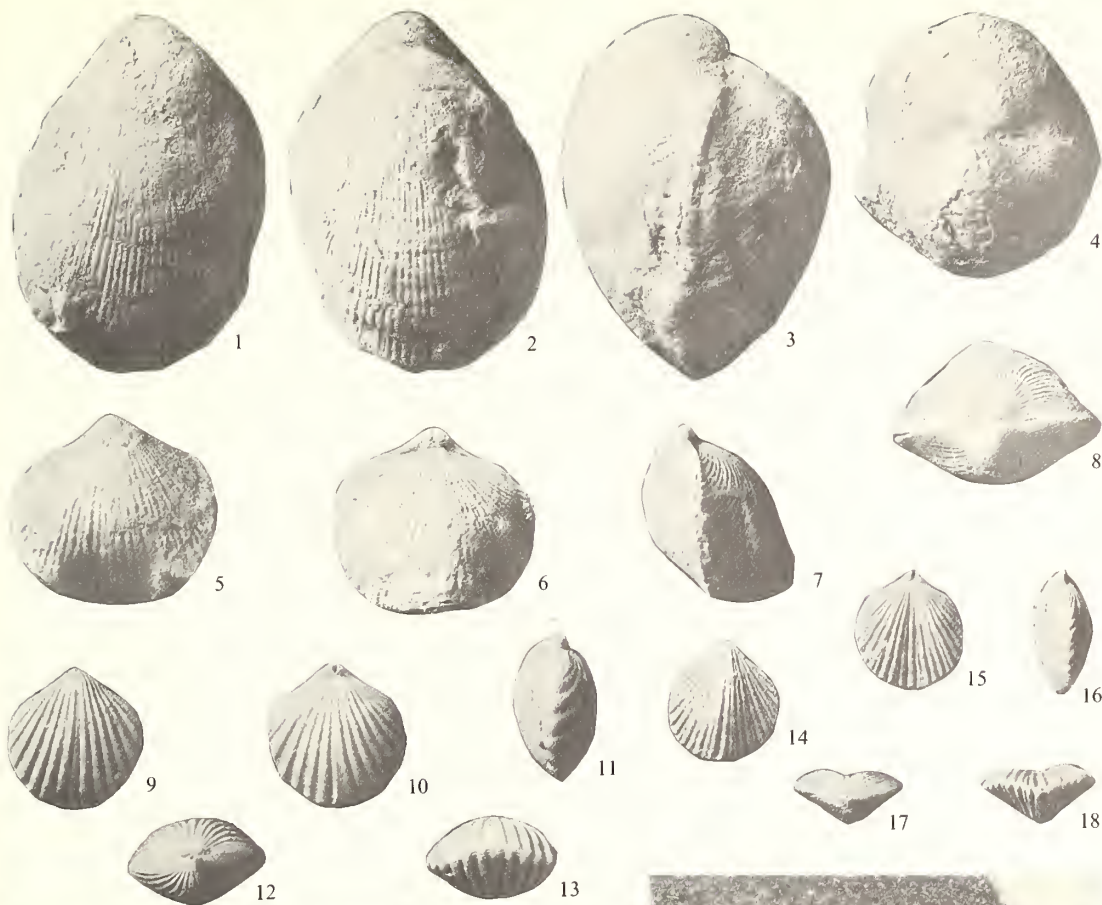
All figures $\times 2$, except figs. 19–20 approx. $\times 40$.

Figs. 1–4. *Nalivkinia (Nalivkinia) gruenewaldtiaformis* (Peetz, 1901). GS 45398 hypotype, ventral, dorsal, lateral, and posterior views of adult. Note that ribs have few anterior growth interruptions and lack frilly projections. Sara-chumysk, Salair, U.S.S.R. (locality K6710 Kulkov); marly limestones, Wenlock. Figs. 5–8. *Nalivkina (Anabaria) rara* (Nikiforova, 1961). GS 45397 hypotype, ventral, dorsal, lateral, and posterior views of adult specimen. Ribs are tubular, lack frills. Omnutakh River, Siberian Platform, U.S.S.R. Wenlock.

Figs. 9–13, 20. '*Clintonella*' *anticostiana* (Twenhofel, 1928). 9–13, GS 45399 hypotype, ventral, dorsal, lateral, posterior, and anterior views. Note lack of carination, accentuated mid-ribs. 20, GS 45392, photomicrograph of hinge plate and tooth structure (serial peel). NTS Jupiter River 75140:87850, Jupiter Formation (Zones 6–7), Anticosti Island, Canada. Upper Llandovery.

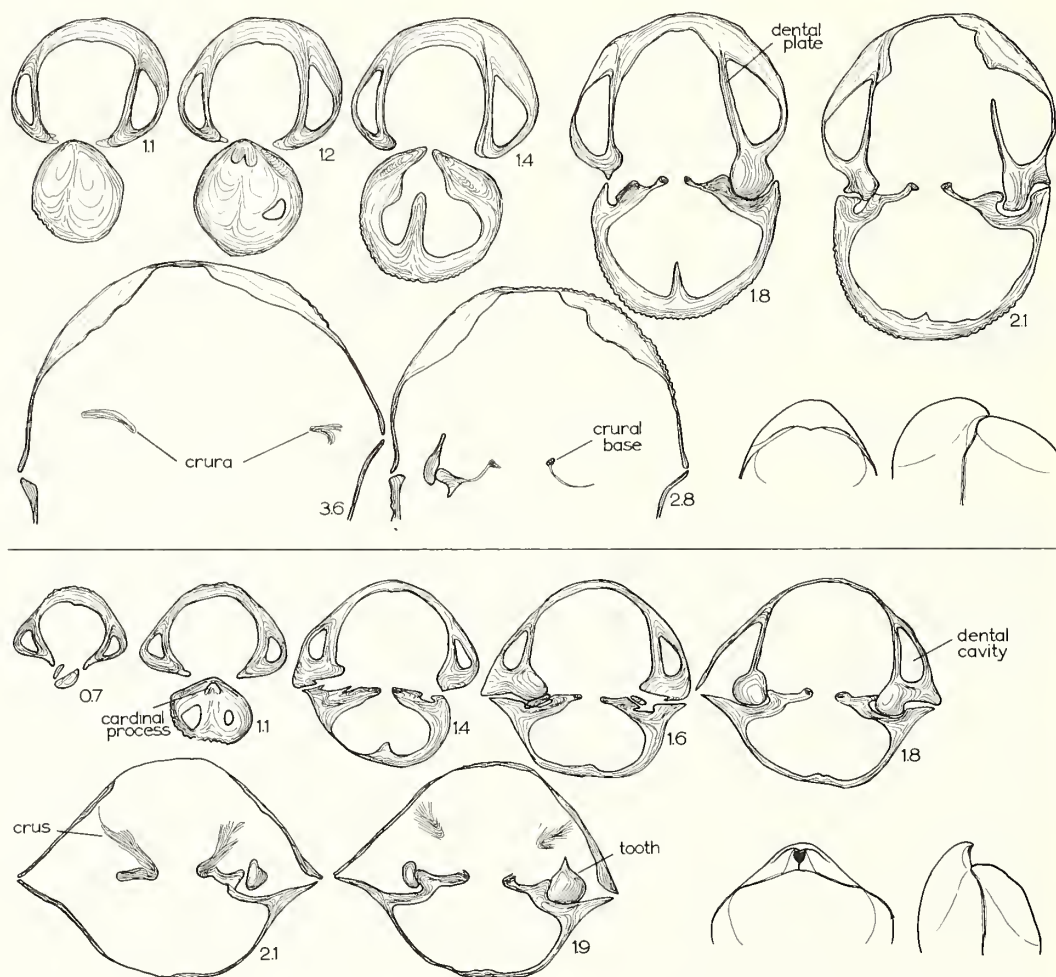
Figs. 14–18. *Alispira gracilis* Nikiforova, 1961. GS 45400 hypotype, ventral, dorsal, lateral, posterior, and anterior views of adult specimen. Note the carination, resulting in dorsal sulcus (contrast with figs. 9–13). Podkamennaya River, Tunguska, Siberian Platform, U.S.S.R. Llandovery.

Fig. 19. *Catazyga headi headi* (Billings, 1862). GS 45397 hypotype, photomicrograph of serial peel showing crural base (cb), hinge plate and tooth (t). NTS Bécancour 01450:38880, Pontgravé River Formation, Canada. Ashgill.



vertically aligned teeth, thin, horizontally aligned socket plates, delicate crural bases, and fibrous crural tips (text-fig. 16). Material sectioned was from the syntype collection of Peetz located in the Museum of the Historical Geology Section of Leningrad University, and made accessible by E. S. Poretskaya. The large syntype collection shows that a gradation exists in external morphology between the type species and the syntopic species *N. sibirica* Bublichenko, 1927.

Nalivkinia (*Nalivkinia*) has not been found on the Siberian Platform, in the Baltic region, or in Britain, and seems to be limited to the southern and Asiatic parts of the U.S.S.R. Its restricted distribution is comparable to *Tuvaella*. An external rib structure like *Nalivkinia* occurs in some atrypids from Anticosti Island, Canada, but internally these are very different.



TEXT-FIGS. 16-17. Serial sections of *Nalivkinia gruenewaldtiaeformis* (Peetz, 1901); (top), GS 45376, Wenlock, Sara-chumysk, Salair, U.S.S.R.; and *Anabaria rara* (Nikiforova, 1961) (bottom), GS 45375, Wenlock, Omnutakh River, Siberian Platform, U.S.S.R. Scale $\times 5$.

Genus NALIVKINIA Bublichenko, 1927
Subgenus ANABARIA Lopushinskaya, 1965

Plate 40, figs. 5-8; text-fig. 17

Type species. Catazyga(?) rara Nikiforova and Andreeva, 1961 (pp. 248-249, pl. 54, figs. 1-7). Wenlock, south-west Siberian Platform, Omnutakh River, U.S.S.R.

Remarks. Lopushinskaya (1965) correctly saw the affinity of *Catazyga(?) rara* to the genus *Nalivkinia*. The type species of *Nalivkinia*, *N. gruenewaldtiaeformis* (Peetz, 1902) differs only slightly in its internal structure from the species *rara* (see this text). The only difference lies in external form, and in shell-wall thickness, which could be an infrageneric character. Externally, *Anabaria* has a less-incurved beak and a slightly flatter shell with broad sinus. The internal similarities are so striking that it is hard to tell them apart. Except for jugal processes and spiralia, which were not present in the material sectioned, the following items were identical in the two taxa: large dental cavities and straight hair-line structure (dental plate s.s.) on the inner side of the tooth, deltidial plates (small, hollow apically), cardinal process (thin lining in notothyrial pit), distinct thin socket plates, small crural bases expanding into thick, curved, feathery crura (text-fig. 17). The internal affinities of both *Nalivkinia* and *Anabaria* are with *Desquamatia* of the Devonian; internally *Nalivkinia* and *Anabaria* are so much alike it is probably better to classify them under the same genus and even subgenus. Beak incurvature is variable in the Sara-chumysk collections of Peetz. Beak incurvature and shell form are also infraspecifically different in Devonian taxa. However, until the jugal processes and spiralia are better known, it may be advisable to follow Lopushinskaya's separation. In looking at the serial sections particular attention should be paid to comparisons of *gruenewaldtiaeformis* and *rara* (text-fig. 17).

Species assigned to Nalivkinia (Anabaria).

?*Nalivkinia kazachica* Borisyak, 1955 (pp. 61-63, pl. 10, fig. 3; pl. 11, figs. 17-19; pl. 13, figs. 1-3). Silurian, Central Kazakhstan, U.S.S.R. Lateral cavities and 'dental plates' seem to indicate *Anabaria* affinities.

?*Nalivkinia kassini* Borisyak, 1955 (pp. 63-64, pl. 10, figs. 1-2; pl. 13, figs. 6-7). Silurian, Central Kazakhstan, U.S.S.R. Serial sections not definitive.

?*Nalivkinia rhomboidalis* Borisyak, 1955 (pp. 64-65, pl. 10, figs. 10-13; pl. 13, figs. 4-5). Silurian, Central Kazakhstan, U.S.S.R. More coarsely ribbed, possibly an *Alispira*.

Genus ALISPIRA Nikiforova, 1961

Plate 40, figs. 14-18; text-fig. 18

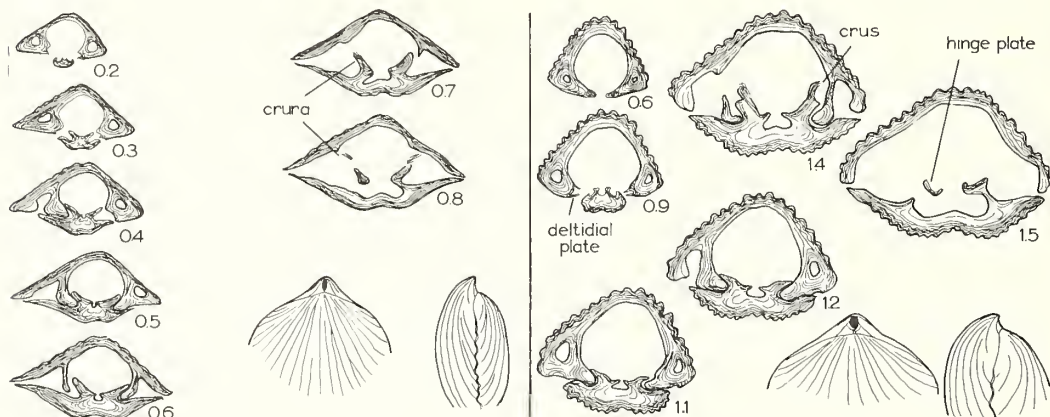
Type species. Zygospira (Alispira) gracilis Nikiforova, 1961, pp. 244-247, pl. 53, figs. 1-8; text-fig. 41.

Range. Llandovery-Wenlock.

Distribution. U.S.S.R. (Siberian Platform, Estonia). Not known from Britain, the Baltic, or other well-known Llandovery-Wenlock sections.

Remarks. The atrypoid relationships of this genus are without doubt, as confirmed by Nikiforova (1961) and Nikiforova and Modzalevskaya (1968). However, since the detailed internal structure of the poorly preserved, synchronous North American

genus *Clintonella* is yet unknown (see Boucot and Johnson 1970), doubt remains if *Alispira* is a junior synonym of *Clintonella*. If both taxa are characterized by carination, and if internal structures are similar, there may be no way of telling them apart. Clinton-age material in eastern North America is generally either silicified or preserved as moulds and casts, and sheds no light on the significant internal structures. The Jupiter River Formation of Canada yields *Homeospira anticostiata* which is probably atrypoid (see Pl. 40, fig. 20; text-fig. 19); but whether this is synonymous with *Clintonella* is not clear, since the Anticosti material lacks carination. Serial sections of topotypic *Alispira* (text-fig. 18) and the Anticosti material of '*Clintonella*' (text-fig. 19) is compared side by side. Note the disposition of the hinge plate and crura in both species.



TEXT-FIGS. 18–19. Serial sections of *Alispira gracilis* (Nikiforova, 1961); (left), GS 45382 from the Podkamennaya River, Tunguska, Siberian Platform; Llandovery; (right), *Clintonella? anticostiata* (Twenhofel, 1928), NTS Jupiter River 75140:87850; Zones 6–7, Jupiter Formation (Upper Llandovery). Compare the apical structures in the two species. Scale $\times 5$.

Genus CLINTONELLA Hall and Clark, 1893

Type species. *Clintonella vagabunda* Hall and Clarke, 1893, pp. 159–161, pl. 52, figs. 1–11. Original material derived from 'drifted and decomposed block of sandstone found without label among the collections presented to the New York State Museum'. Probably derived from the Clinton group in Orleans county (ibid., p. 161).

Range distribution. Llandovery and possibly Wenlock, North America.

Remarks. The affinity of this genus is still unsettled. Hall and Clarke (1893) intimated a close relationship with *Zygospira* on the basis of the hinge plate and muscle impressions. However, they stated that no spiralia had been found in any material examined. Boucot and Johnson (1970), despite new material, came no closer to an answer on affinities, since they, like Hall and Clarke before them, failed to find spiralia. Nevertheless, they were able to establish a more precise age for some *Clintonella* specimens, namely Llandovery C_3 to C_4 , though leaving open the question of relations with the Zygospiridae or Atrypidae. *Clintonella* has affinities with the Siberian Llandovery *Alispira* Nikiforova, 1961 in sharing a carinate pedicle valve and sulcate

brachial valve (see Pl. 40, figs. 14–18 for topotypic material of *Alispira*). This carination is not always marked in illustrated material of *A. gracilis tennicostata*. *Alispira* possesses dental cavities, dorsal atrypoid spiralia, postero-ventral jugal processes (separated), and somewhat unusual hinge plates (see Modzalevskaya's serial sections in Nikiforova 1961, p. 246; compare with text-fig. 18). Nikiforova pointed out that some North American '*Homeospira*', e.g. '*H.* *anticostiana*' Twenhofel, 1928 and *H. subcircularis* Savage, 1913 were similar to *Alispira*. This is a problem still under investigation, particularly in regard to Anticosti material (Pl. 40, figs. 9–13, 20; text-fig. 19). A number of North American taxa assigned to '*Homeospira*' may be true atrypoids, and may belong to a new genus of clintonellinid lacking carination of any kind. Provisionally it is better to retain North American atrypoids of this type under *Clintonella*.

Clintonella? anticostiana (Twenhofel, 1928)

Plate 40, figs. 9–13, 20; text-fig. 19

1928 *Homeospira anticostiana* Twenhofel, p. 220, pl. 20, figs. 1–3.

Remarks. Text-fig. 19 serializes the apical structures of a typical specimen from Anticosti Island. Calcified material has not yet revealed spiralia. Dental cavities are distinct, small deltidial plates about the apex of the brachial valve, teeth are dorso-medially directed and simple in design. The hinge plate is somewhat similar to *Alispira*, but crura develop rather differently from crural bases (see Pl. 40, fig. 20; text-fig. 18). The inner part of the hinge plate is unique for atrypoids, in having medially pointed blades; the significance of this is not clear. Some *Alispira* (e.g. *A. rotundata* Nikiforova and Modzalevskaya, 1968, pp. 59–61, pl. 2, figs. 1–7) also have a similar hinge plate development.

CONCLUSIONS

Before atrypoid taxonomy can reach a satisfactory major scheme, a number of problems need to be solved. Most of these solutions rest on a better knowledge of internal structures, especially of the brachidia and pedicle structures. The theme of this paper is that the early atrypoids, the Zygospiridae (mostly of Ordovician age), were all 'designed' with a similar dorso-medially pointed spiralia and a dorsal, fused jugum. This implies a common method of solving the problems of food-gathering and waste disposal. In terms of external morphology, the zygospirids lacked many of the refinements of the Devonian atrypoids (the Silurian representing a transitional stage in morphology). Zygospirids did not develop specializations for settling or anchoring on soft muddy bottoms (e.g. frills, spines, planation or elongation of one or both valves, cementation, pedicle peculiarities). The zygospirinids were probably the ancestors of the Atrypidae, the tuvaellinids possibly of the Carinatininae, and the catazyginids were possibly the ancestors of the Palaferellinids (s.s.) and the Karpinskiinids. Knowledge is needed of the interior of different species assigned at various times to transitional generic forms, e.g. '*Eospirigerina*', '*Clintonella*' (or '*Homeospira*'), '*Alispira*', '*Zygospira*', etc. There is ample scope for further work.

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CORALLIAN (UPPER JURASSIC) MARINE BENTHIC ASSOCIATIONS FROM ENGLAND AND NORMANDY

by F. T. FÜRSICH

ABSTRACT. Using the trophic group approach, seventeen macroinvertebrate and one trace-fossil association have been described quantitatively, using 170 bulk collections, from the Middle and Upper Oxfordian of Normandy, Dorset, Oxfordshire, and Yorkshire. Most associations are dominated by bivalves and gastropods, whilst echinoderms and brachiopods are less important. Sedimentary and biostratigraphic evidence indicate that, with few exceptions, the associations are the autochthonous or parautochthonous relics of ancient communities. The taphonomy and environments of each association have been discussed and comparisons have been drawn with other Mesozoic benthic associations. The highly abundant oyster *Nanogyra nana* is interpreted as an opportunistic species and the abundance of the pectinid *Chlamys* is regarded as a feature typical of Corallian faunas. The scarcity of brachiopods, which are also uncommon elements in many other Jurassic and Cretaceous benthic faunas, is thought to be related to the short dispersal time of their larvae, combined with competition by bivalves and changing environments.

PALAEOECOLOGY, and especially studies of ancient communities triggered off by research in modern ecology have increasingly gained popularity amongst palaeontologists. Besides the classic work of Petersen (1913) on the fauna of the North Sea and that of Thorson (e.g. 1933, 1957) it is on studies of Russian workers like Turpaeva (1948, 1949, 1957; see also Neyman 1967) that methods and approach in palaeosynecological studies are based. Studies of communities include the description of their composition and structure and their relationship to the environment. Generally, these aspects can best be studied on Recent communities whilst another aspect, that of community evolution, represents the main contribution of the palaeontologist to the field of synecology. The aim of this paper is to contribute to this last aspect of community studies, although it can serve only as a small contribution to a framework of data which will eventually enable us to test concepts now in vogue. Studies of ancient communities or associations (the latter term is preferred for reasons given below) have been mainly on the Palaeozoic (e.g. Boucot 1975; Bretsky 1969, 1970; Hurst 1975; Walker and Laporte 1970; Ziegler *et al.* 1968) and on the Cretaceous (e.g. Kauffman 1967; Rhoads *et al.* 1972; Scott 1974). For the Jurassic, invertebrate associations have been described quantitatively only recently (Wright 1973, 1974; Duff 1975), the bulk of palaeosynecological work being only semi-quantitative (e.g. Hallam 1960, 1967; Sellwood 1972).

The purpose of the paper is to give a quantitative description and environmental interpretation of the seventeen macroinvertebrate and one trace-fossil association which have been recognized. Sedimentary and biostratigraphic evidence has been used to establish the taphonomy and general environment of each association. Using this basic information, facies and substrate relationships of the fauna have been investigated and the results published separately (Fürsich 1976a, b).

Geological setting. The Corallian (Middle and Upper Oxfordian; text-fig. 1) stretches from Yorkshire down to Dorset in England and also in Normandy, France (text-fig. 2). The main sections under study were provided by cliffs in Yorkshire (Filey Brigg), Dorset (Bouleaze Cove, Osmington Mills to Ringstead Bay, Shortlake to Black Head, Sandsfoot Castle, East Fleet), and Normandy (Houlgate to Villerville). Additional information, especially on the reef facies, was gained in quarries in the Vale of Pickering, Yorkshire, in Oxfordshire, and in Berkshire (for a list of the localities see appendix).

In Dorset, the Corallian consists of four limestone-clay-sand cycles (Talbot 1973), separated partly by erosion surfaces. These cycles correspond to regressing sequences, the erosion surfaces marking renewed transgressions. The sediments were laid down in a shallow sea, probably in the upper shelf region, and the main facies types comprise offshore calcareous sands and carbonates, oolite banks, nearshore muds, subtidal sand bars, lagoonal muds, intertidal sands, estuarine sands and muds, and nearshore ferruginous oolitic muds. The sediments of the Corallian of Yorkshire (sands, mixed limestones, oolites, and patch reefs) and Normandy (similar in lithology to Dorset) have received less attention, and one purpose of the study was to apply the palaeoecological evidence, tested in the well-known Dorset section, to these two areas (Fürsich 1976*b*).

Previous work. There are several prerequisites to a palaeosynecological study: stratigraphical studies to facilitate correlations; sedimentological studies to define environments; and taxonomic studies to interpret the autecology of the faunal elements. For the Corallian, these prerequisites have been largely fulfilled. Blake and Hudleston (1877), Hudleston (1878), Arkell (e.g. 1927, 1933, 1935-1948, 1936), Wilson (1933, 1949), Callomon (1960), and Wright (1972) have dealt with the stratigraphy, whilst Twombly (1964), Wilson (1968*a, b*), Lee (1971), Brookfield (1973*a*), and Talbot (1973, 1974) have developed various sedimentological models for the Yorkshire and Hampshire Basins. The bivalves, the bulk of the fauna, have been described by Arkell (1929-1937), and the trace fossils by Fürsich (1974). Microfaunal studies have been carried out by Whatley (1965), Gordon (1965), and Guyader (1968). (For an extensive bibliography see Brookfield 1973*a*.) First attempts to distinguish faunal assemblages have been made by Arkell (1929-1937) who recognized, for example, a bivalve assemblage typical of the reef environment. Arkell (1928, 1935) also dealt with the ecology of the Corallian patch reefs in a more general way. The trace-fossil fauna has been interpreted in terms of distribution patterns and environmental significance by Fürsich (1975). Otherwise, no ecological studies have been undertaken.

TEXT-FIG. 1. Composite sections of the Corallian of the main areas under study; adapted from Fürsich (1975). C.O.F. = Calcaire à oolithes ferrugineuses; OOL. D. TROUVILLE = Oolithe de Trouville à *Nucleolites scutatus*; F. 'CORAL RAG' D. TROUVILLE = Facies 'Coral Rag' de Trouville; C. HENN. = Calcaire de Hennequeville; A.N. VILL. = Argiles Noires de Villerville; O.C. = Oxford Clay; THB = '*Trigonia* hudlestoni' Bed; BENCL. G. = Bencliff Grit; TRIG. CLAV. B. = '*Trigonia* clavellata' Beds; SANDSF. C. = Sandsfoot Clay; SANDSF. G. = Sandsfoot Grit; R.W.C. = Ringstead Waxy Clay; K.C. = Kimmeridge Clay; L. CALC. GRIT = Lower Calcareous Grit; P.B. = Passage Beds; HAM. O. = Hambleton Oolite; M. CALC. GRIT = Middle Calcareous Grit; M.O. Malton Oolite.

Geological column diagram showing stratigraphic units. The column is divided into sections with different patterns: horizontal lines, dots, wavy lines, and cross-hatching. Dashed lines indicate boundaries or unconformities. The units are labeled as follows:

- O.C. NOTHE GRITS
- THB N. CL.
- BENCL G.
- OSMINGTON OOLITE GROUP
- TRIG. CLAV. B.
- SANDSF. C.
- SANDSF. G.
- R.W.C.
- K.C.
- C. HENN
- A.N. VILL.

pseudocordata
decipiens
cautisnigrae
transversarium
plicatilis
cordatum

L. CALC. GRIT P.B. HAM. O. M. CALC. G. M.O.

1

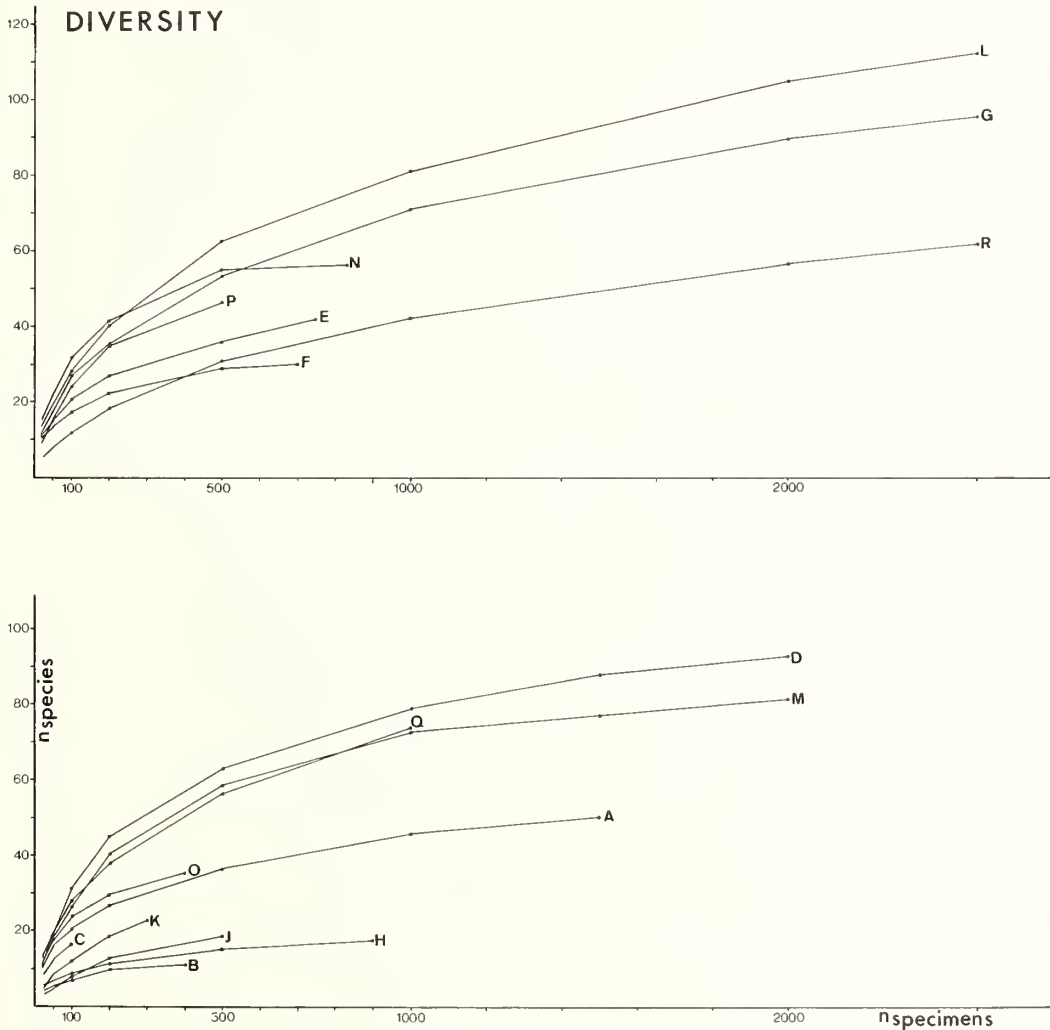
- | | |
|---|----------------|
|  | clay, marl |
|  | silt |
|  | sand |
|  | arg. limestone |
|  | limestone |
|  | oolite |

10 m



TEXT-FIG. 2. Outcrop of Upper Jurassic rocks in England and Normandy.

Material and methods. One hundred and seventy bulk collections with more than 30 000 fossils were used for this study. The collections were broken up partly in the field, partly in the laboratory and all macrofossils were saved. For bivalved animals, the fauna has been totalled by counting only the most numerous valve together with the articulated specimens. Preservation, fragmentation, encrusters and borers, size sorting, and relationship between right and left valves in bivalved animals were noted. Orientation of shells, especially with respect to life position was recorded as were the trace-fossil fauna, sedimentary structures, and diagenetic features. The diversity of the samples has been measured using Sanders's (1968) rarefaction method (text-fig. 3). For grouping the collections into associations the trophic group approach



TEXT-FIG. 3. Diversity of Corallian benthic associations expressed by rarefaction curves (Sanders 1968).

has been selected. Firstly, for each collection the trophic nucleus consisting of the numerically dominant species which make up 80% of the fauna (Neyman 1967) was constructed. Then collections with an identical or similar trophic nucleus were grouped into associations. Each of these associations is characterized by one or more species which reach here the peak of their distribution (text-fig. 4). In addition, the associations differ in their trophic nucleus, and in most cases exhibit a distinct ecological composition (e.g. text-fig. 6). The trophic group analysis, developed in Russia by Turpaeva (1948), has been discussed by Walker (1972) and applied to fossil material, for instance by Rhoads *et al.* (1972) and by Duff (1975). Rhoads *et al.* (1972) also discuss the drawbacks of this method when applied to fossil faunas, as biomass and original composition of the fauna have been lost. Walker (1972) suggested substituting biovolume for biomass when working with fossil samples and for this purpose, size histograms for the members of the trophic nuclei are given (e.g. text-fig. 7). The feeding levels usually recognized in trophic group analysis (Walker and Bambach 1974) have been augmented by the introduction, in intermediate position, between low-level and high-level suspension feeders, of medium-level suspension-feeders represented mainly by the bivalves *Pinna* and *Gervillia*. This was thought necessary to account for the dense feeding stratification realized in the associations which are nearly all dominated by suspension-feeders. Pendent bivalves like *Meleagrinella*, *Oxytoma*, and probably also *Pteroperna pygmaea* were—in contrast to Duff (1975)—included into the benthos as high-level suspension-feeders, because their distribution is governed by the presence of seaweed or algae which in turn is influenced by substrate conditions.

The Corallian faunas lack (as do most fossil samples) soft-bodied animals. Where possible, trace fossils have been used to compensate for this but they are no real substitute. The term 'community' therefore cannot be applied to these samples and the term 'association', meaning a non-random, recurrent assemblage of fossils usually representing the remnant of a community, is preferred (see also Fürsich 1975; Duff 1975). For each association, the degree of distortion from the original community is discussed using biostratigraphic and sedimentological data. The *autecology* of the bivalves was derived using the morphology of the hard parts and comparison with Recent species (based mainly on Stanley 1970, 1972). Hard parts of gastropods are far less indicative of a particular mode of life and often species of the same genus occupy completely different niches. Because of this, the reconstructed life habits of Corallian gastropods are often conjectural and open to criticism. For each association, the autecology of the members of the trophic nucleus has been presented in an attempted reconstruction of the ancient community (e.g. text-fig. 5).

TEXT-FIG. 4. Numerical abundance of the most important Corallian body fossils in the various benthic macroinvertebrate associations (A–R). Dark stippling: association for which a species exhibits a pronounced preference and thus is highly characteristic; light stippling: associations in which a species preferentially occurs (usually not more than two); these species are less specific but still useful for defining associations. The nearly ubiquitous *Nanogyra nana* has been regarded as a very characteristic species where it represents more than 80% of the fauna (R) and as an accessory species where it represents more than 50% of the fauna (G, H). Torqu. = *Torquirhynchia inconstans*; the other bar in the same column represents *Thurmanella*.

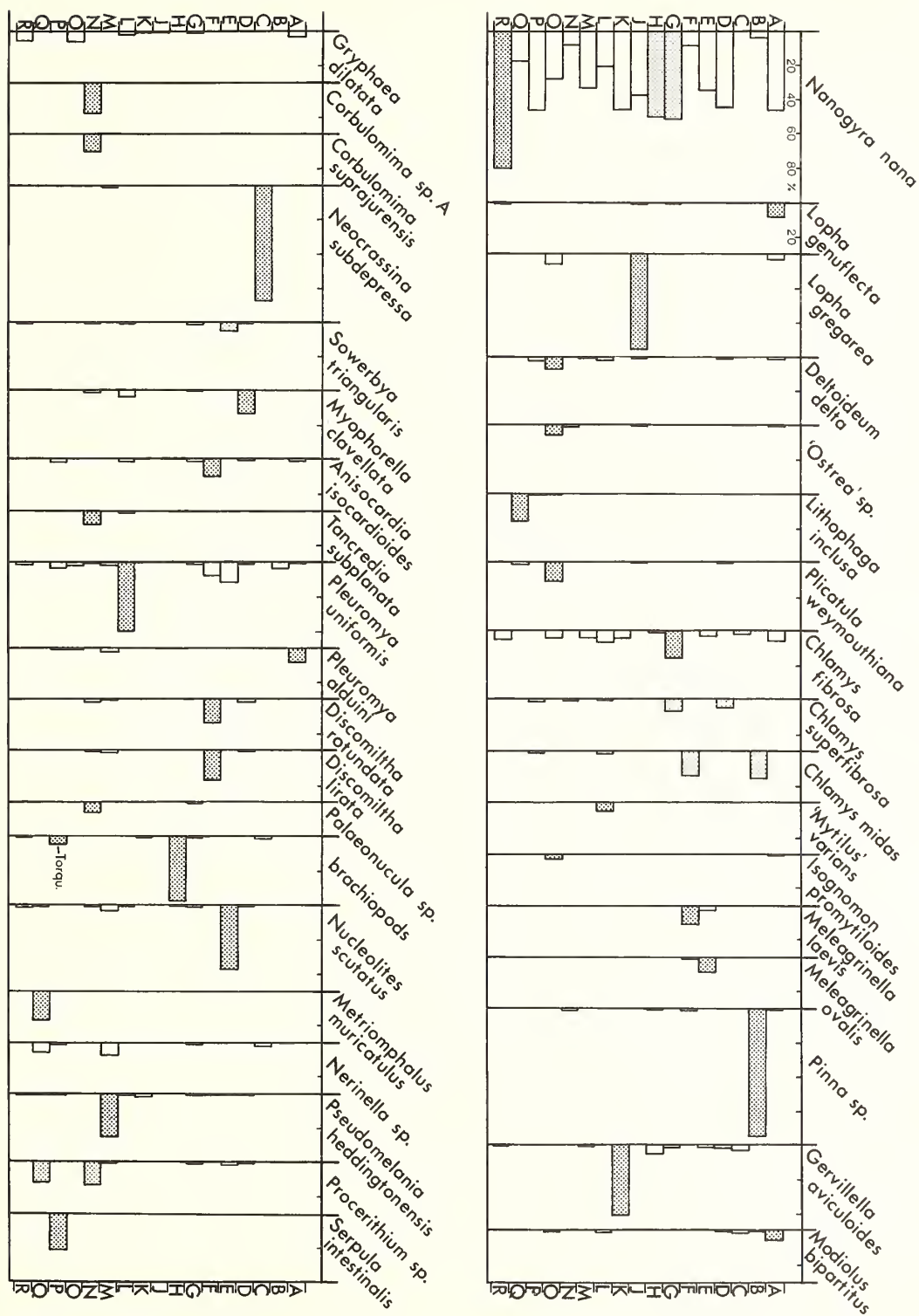


TABLE 1. *Modiolus bipartitus*/*Pleuromya alduini* association (A). (Similar tables of data for the remaining sixteen associations have been deposited with the British National Library, deposition SUP 14007.) Eighteen collections. 1798 specimens.

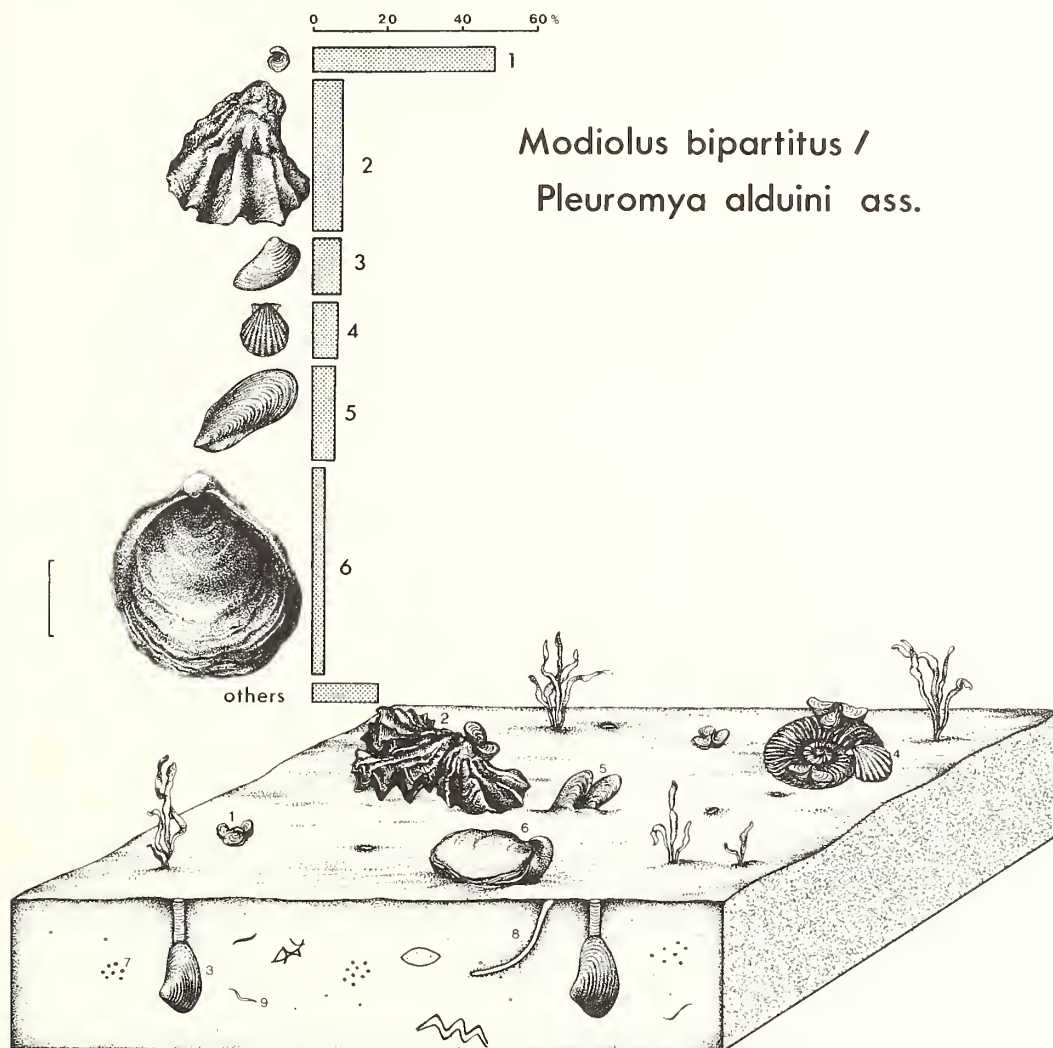
Composition of fauna (members of the trophic nucleus are marked with an asterisk):

bivalves (98-94%):	%	Pres. %		%	Pres. %
* <i>Nanogyra nana</i> (J. Sowerby)	48.66	0.83	<i>Placunopsis duriuscula</i> (Phillips)	0.05	0.05
* <i>Lopha</i> (A.) <i>gemuslecta</i> Arkell	8.17	0.55	<i>Nuculana</i> (N.) sp.	0.05	0.05
* <i>Pleuromya alduini</i> (Brongniart)	7.89	0.83	<i>Myopholas</i> sp.	0.05	0.05
* <i>Chlamys</i> (R.) <i>fibrosa</i> (J. Sowerby)	7.17	0.66	<i>Arcomytillus pectinatus</i> (J. Sowerby)	0.05	0.05
* <i>Modiolus bipartitus</i> J. Sowerby	6.50	0.83	<i>Praexogyra</i> sp.	0.05	0.05
* <i>Gryphaea</i> (B.) <i>dilatata</i> (J. Sowerby)	3.50	0.83	<i>Plagiostoma rigidum</i> (J. Sowerby)	0.05	0.05
<i>Lopha</i> (A.) <i>gregarea</i> (J. Sowerby)	3.05	0.78			
<i>Pholadomya aequalis</i> J. de C.			gastropods (0.16%):		
Sowerby	2.66	0.50	<i>Bathrotomaria</i> sp.	0.11	0.05
<i>Anisocardia isocardioides</i> (Blake and Hudleston)	1.39	0.28	<i>Purpurina</i> sp.	0.05	0.05
<i>Pinna lanceolata</i> J. Sowerby	1.22	0.22	brachiopods (0.32%):		
<i>Pleuromya uniformis</i> (J. Sowerby)	1.11	0.44	' <i>Rhynchonella</i> ' sp.	0.16	0.05
<i>Deltoidum delta</i> (Smith)	1.05	0.11	<i>Thurmanella</i> sp.	0.11	0.11
<i>Homomya</i> sp.	0.88	0.33	' <i>Terebratula</i> ' sp.	0.05	0.05
<i>Isognomon promytiloides</i> Arkell	0.83	0.17			
<i>Isognomon</i> sp.	0.44	0.39	serpulids (0.55%):		
<i>Limatula elliptica</i> (Whiteaves)	0.44	0.28	<i>Serpula</i> (<i>Dorsoserpula</i>) <i>sulcata</i>		
<i>Myophorella</i> sp.	0.38	0.22	J. Sowerby		0.11
<i>Goniomya literata</i> (J. Sowerby)	0.27	0.28	<i>Serpula</i> (<i>Dorsoserpula</i>) sp.		0.44
<i>Oxytoma expansa</i> (Phillips)	0.22	0.55	<i>Serpula</i> (<i>Cycloserpula</i>) <i>intestinalis</i>		
<i>Quenstedtia davisii</i> Arkell	0.22	0.55	Phillips	0.55	0.16
<i>Protocardia dyonisea</i> (Buvignier)	0.22	0.55	<i>Serpula</i> (<i>Cycloserpula</i>) sp.		0.16
' <i>Ostrea</i> ' sp.	0.22	0.11	<i>Serpula</i> (<i>Pentaserpula</i>) sp.		0.11
<i>Pholadomya protei</i> (Brongniart)	0.16	0.17			
<i>Parallelodon aemulum</i> (Phillips)	0.16	0.11	miscellanea:		
<i>Meleagrinella ovalis</i> (Phillips)	0.16	0.11	<i>Nubeculinella</i> sp.		0.94
<i>Cercomya undulata</i> (J. de C.			' <i>Cidaris</i> ' spines		0.05
Sowerby)	0.16	0.05			
<i>Isocyprina</i> sp.	0.16	0.11	trace fossils:		
<i>Cucullaea contracta</i> Phillips	0.11	0.11	<i>Planolites</i> sp.		0.50
<i>Plicatula weymouthiana</i> Damon	0.11	0.11	<i>Chondrites</i> sp.		0.55
<i>Mactromya aeste</i> (d'Orbigny)	0.11	0.11	pyritic tubes		0.61
<i>Placunopsis radiata</i> (Phillips)	0.11	0.11	<i>Talpina</i> sp.		0.11
<i>Protocardia intexta</i> (Muenster)	0.11	0.05			
<i>Trautscholdia</i> cf. <i>Tr. cordata</i>			ecological composition:		
(Trautschold)	0.11	0.11	epifauna: 75.87%		
<i>Chlamys</i> (Chl.) <i>splendens</i> (Dollfus)	0.11	0.11	semi-infauna: 7.73%		
<i>Thracia depressa</i> (J. de C. Sowerby)	0.11	0.11	infauna: 16.34%		
<i>Camptonectes</i> (C.) <i>lens</i>					
(J. Sowerby)	0.05	0.05	biostratinomic data:		
<i>Sowerbya triangularis</i> (Phillips)	0.05	0.05	uncemented fauna in life position: 4.63%		
<i>Entolium corneolum</i> (Young and Bird)	0.05	0.05	bivalved fauna preserved with both valves: 22.85%		
<i>Pteria</i> sp.	0.05	0.05	encrusted: 19.35% of the fauna		
<i>Corbulomima</i> sp.	0.05	0.05	bored: 1.11% of the fauna		
			fragmentation: 50-95%		

CORALLIAN MACROINVERTEBRATE ASSOCIATIONS

A. *Modiolus bipartitus*/*Pleuromya alduini* association

Description. Eighteen collections with altogether 1798 specimens can be attributed to this association (Table 1). Six bivalves (text-fig. 5) form the trophic nucleus with *Nanogyra nana* making up nearly 50% of the fauna whilst *Lopha genuflecta*, *Pleuromya alduini*, *Chlamys (R.) fibrosa*, *Modiolus bipartitus*, and *Gryphaea dilatata* comprise the rest. Three species (*P. alduini*, *L. genuflecta*, *M. bipartitus*) are characteristic of this association (i.e. they reach in it by far the peak of their distribution). Bivalves account for 98.9%

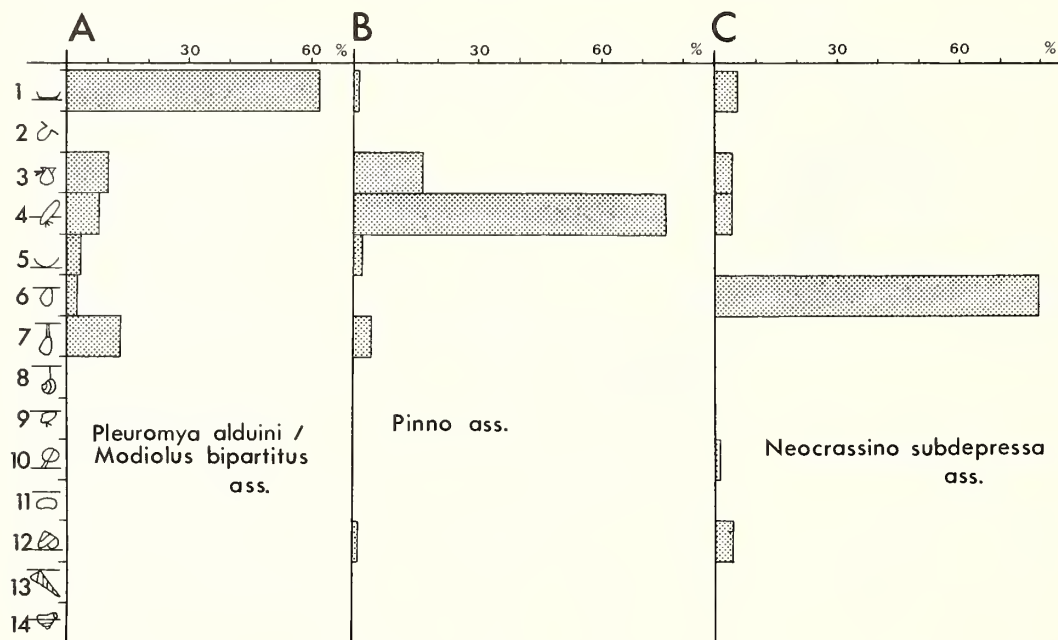


TEXT-FIG. 5. Trophic nucleus and attempted reconstruction of the *Modiolus bipartitus*/*Pleuromya alduini* association (A). Percentage figures give numerical abundances of the various faunal elements. Length of bar: 4 cm. 1, *Nanogyra nana*; 2, *Lopha genuflecta*; 3, *Pleuromya alduini*; 4, *Chlamys fibrosa*; 5, *Modiolus bipartitus*; 6, *Gryphaea dilatata*; 7, *Chondrites* sp.; 8, *Planolites* sp.; 9, pyritic tubes; benthic algae hypothetical.

of the fauna; the remaining groups are gastropods (0.2%), brachiopods (0.3%), and serpulids (0.5%). Echinoderms are only represented by some cidarid spines. Ammonites (mainly *Cardioceras s.l.* and *Aspidoceras*) are common, belemnites rare. Both these groups have not been included in the statistics as they do not belong to the benthos. The trace-fossil fauna (present in fourteen collections) is unvaried, the abundance is medium, the diversity low. Only three ichnospecies were found, all of them having been created by deposit-feeders: *Chondrites*, *Planolites*, and pyritic tubes. The over-all diversity of the benthos is medium (text-fig. 3).

Text-fig. 6 shows that more than 60% of the body fauna are epifaunal cemented forms, especially *Nanogyra* and *Lopha*. Deep-burrowing bivalves, mainly *Pleuromya* and *Pholadomya*, account for 13.6% whilst the semi-infaunal *Pinna lanceolata* and *M. bipartitus* form 7.7%. The percentage of epifaunal byssally attached forms is relatively low (9.9%); its main representative is *Chlamys fibrosa*. 4.6% of the uncemented fauna, especially the deep-burrowing *Pleuromya* and *Pholadomya*, occur in life position. 22.8% of the bivalved fauna are preserved with both valves; 19.3% of the fauna are encrusted. The epizoans are the foraminifera *Nubeculinella* (very common), the bivalves *Plicatula weymouthiana*, *Nanogyra nana*, and *L. gregarea*, as well as serpulids of the subgenera *Cycloserpula*, *Dorsoserpula*, and *Pentaserpula*. 1.1% of the fauna are bored by the bivalve *Lithophaga inchoa*, polychaetes, and a phoronid (represented by the ichnogenus *Talpina* (see Voigt 1972)). Fragmentation ranges from 50 to 95%, most collections being near the lower limit. 11.7% of the fauna are preserved as steinkerns, especially aragonitic forms like shallow and deep burrowers as well as the ammonites. *Gryphaea* and *Deltoideum* are occasionally very worn. In some collections, the oyster fauna is covered with a thin Fe-hydroxide film, an indication of long exposure on the sea floor.

Association A occurs in a narrow substrate and facies range, predominantly in the condensed ferruginous facies consisting of argillaceous micrites or calcareous clays with a varying amount of Fe-ooliths.

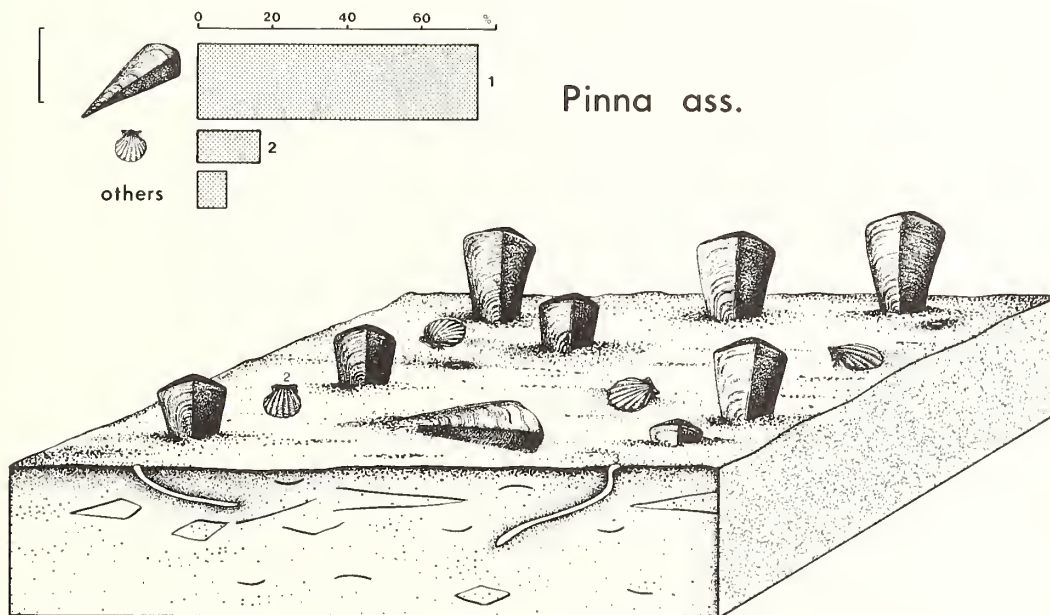


TEXT-FIG. 6. Ecological composition of associations A-C. 1, epifaunal cemented bivalves; 2, boring bivalves; 3, epifaunal byssally attached bivalves; 4, semi-infaunal bivalves; 5, free-resting bivalves; 6, shallow burrowing suspension-feeding bivalves; 7, deep burrowing suspension-feeding bivalves; 8, infaunal bivalves deposit-feeding at the depositional interface; 9, infaunal deposit-feeding bivalves; 10, epifaunal brachiopods; 11, infaunal deposit-feeding echinoids; 12, epifaunal gastropods; 13, infaunal and semi-infaunal gastropods; 14, free-living serpulids.

Discussion. The presence of fauna in life position and the preservation of nearly one-fourth of the fauna with both valves indicate that transport played an insignificant role in the formation of this association. Preservational bias can be ruled out as the aragonitic fauna is still preserved as steinkerns, so that association A can be regarded as the autochthonous part of a true community whose soft parts were removed. Facies, high fossil density, and biostratigraphic evidence point to a very slow accumulation of the sediment under predominantly quiet conditions. This, however, did not lead to a mixing of different superimposed communities as is the case with some collections (described below) but the same communities must have persisted for long periods of time. Slow sedimentation rate probably resulted in a slightly consolidated substrate; this might have been responsible for the absence of any deposit-feeders except in the trace-fossil fauna. Shells lying on the surface provided suitable substrate for initial settlement of the oysters which occur usually in clusters, often several generations settling on top of each other. Three feeding levels may be recognized: infaunal deposit-feeders, represented by the trace fossils, low-level suspension-feeders, e.g. shallow and deep burrowers, and *Chlamys*; and medium-level suspension-feeders, e.g. *Pinna*.

B. *Pinna* association

Description. Six collections with 453 specimens represent this association. *P. sandsfootensis* is by far the dominant species (75.5%) and, together with *Chlamys* (*R.*) *midas*, forms the trophic nucleus (text-fig. 7). *P. sandsfootensis* is confined to this association (see also Arkell 1929-1937) and thus serves as its most characteristic species. *C. midas* is somewhat less specific as it reaches a second peak in its distribution in



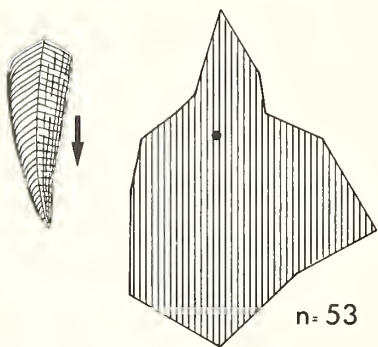
TEXT-FIG. 7. Trophic nucleus and attempted reconstruction of the *Pinna* association (B). Length of bar, 8 cm. 1, *Pinna sandsfootensis*; 2, *Chlamys midas*; 3, *Planolites* sp.

the *Discomiltha* association (F). 99.3% of the fauna are bivalves, the rest gastropods. The only, although abundant, trace fossil occurring with the association is *Planolites*. The over-all diversity is very low (text-fig. 3). Semi-infaunal bivalves (75.9%; i.e. *Pinna*, *Modiolus bipartitus*) dominate the ecological spectrum (text-fig. 6) leaving only 16.8% for the byssally attached epifauna (*Chlamys*). Burrowing forms are rare except *Pleuromya uniformis* (3.9%) which is the only representative of the deep-burrowing bivalves. The virtual absence of the cemented epifauna so abundant in other associations is also striking. 3.3% of the uncemented fauna (mainly *Pinna*) are in life position. The number of bivalved animals with both valves preserved is very high: 73.1%. The fauna is neither bored nor encrusted. Fragmentation varies between 75.0 and 85.0%. Except for most burrowing forms (mainly *Pleuromya*) specimens are preserved with their shell.

All six collections come from medium-grained sandstones of the Sandsfoot Grit (Dorset coast) thus showing a clear relationship between substrate/facies and association.

Discussion. The six collections have been obtained from different horizons within a massive sandstone body. The close similarity of the samples indicate that the *Pinna* association persisted for some time during the formation of the sandstone body. Lack of encrusters and borers indicates that shells did not remain exposed on the sea floor for long and that the rate of sedimentation was thus fairly continuous. The *Pinna* association is the autochthonous relic of a former community which is illustrated by the high percentage of still bivalved specimens and the presence of shells in life position. Numerous flat-lying bivalved *Pinna* evidence short periods of stronger currents or wave movements which led to their excavation *in situ* without further transport. Orientation studies on these flat-lying *Pinna* (text-fig. 8) suggest that either tidal currents or oscillatory wave action were responsible for their excavation.

The *Pinna* association contains two trophic groups: suspension-feeders and deposit-feeders. Three feeding-levels can be distinguished: infaunal deposit-feeders (worms?) represented by *Planolites*, low-level suspension-feeders (e.g. *Pleuromya*, *Ctenostreon*), and medium-level suspension-feeders (*Pinna*).

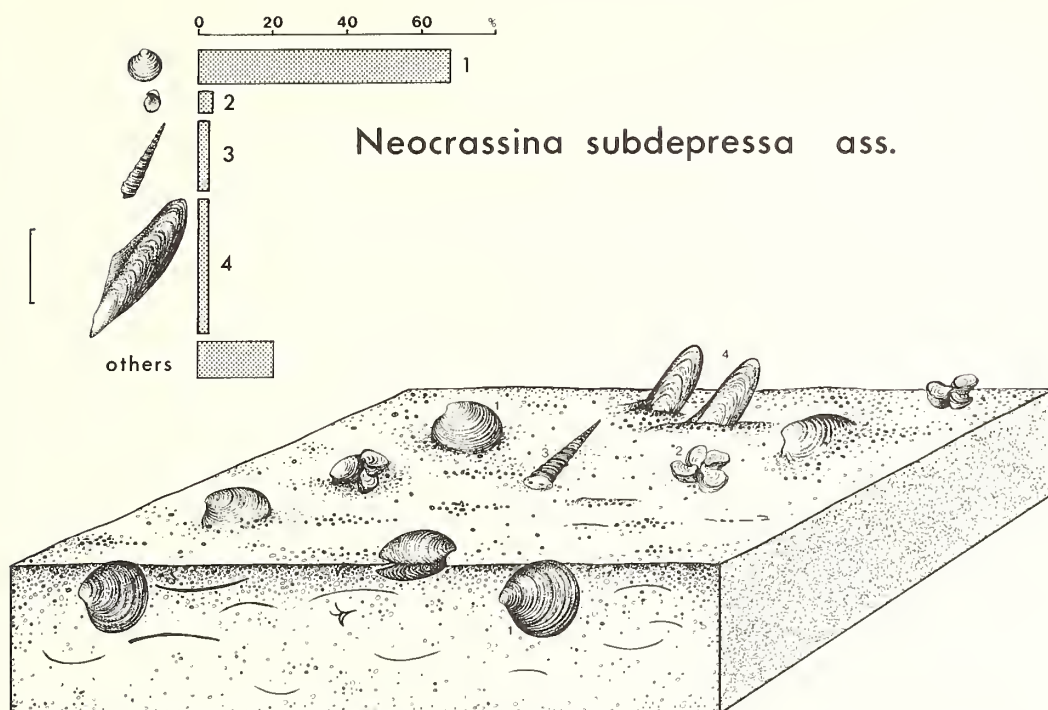


TEXT-FIG. 8. Orientation of flat-lying bivalved *Pinna* in the *Pinna* association. Bedding plane in the Sandsfoot Grit, Sandsfoot Castle, near Weymouth, Dorset.

C. Neocrassina subdepressa association

Description. This association has been found in only one collection with ninety specimens. It is dominated by *N. (N.) subdepressa* (text-fig. 9), a species which occurs in other associations only sporadically. The bivalves *Nanogyra nana*, *Gervillella aviculoides*, and the gastropod *Nerinella* are the remaining members of the trophic nucleus. The bivalves *Perampliata ampliata* (2.2%) and *Fimbria umbonata* (2.2%) occur only rarely in other associations and are thus also characteristic of association C. Again, bivalves dominate the fauna (94.4%) and brachiopods (1.1%) form the rest. No trace fossils are present. Shallow-burrowing bivalves (*Neocrassina*) are the most important ecological group (79.8%; text-fig. 6) whereas byssally attached and cemented epifauna, as well as semi-infaunal bivalves and epifaunal gastropods, share the remaining 20%. No faunal elements are preserved in life position and no bivalves occur with both valves. 11.1% of the fauna are encrusted by *Nanogyra nana* and *Cycloserpula*; borers are missing. Fragmentation is 95%, quite a high value. All specimens, even gastropods, are preserved with their shell; a preservational bias of the fauna can thus be excluded.

The *Neocrassina* association occurs in rubbly, somewhat argillaceous oomicrite.

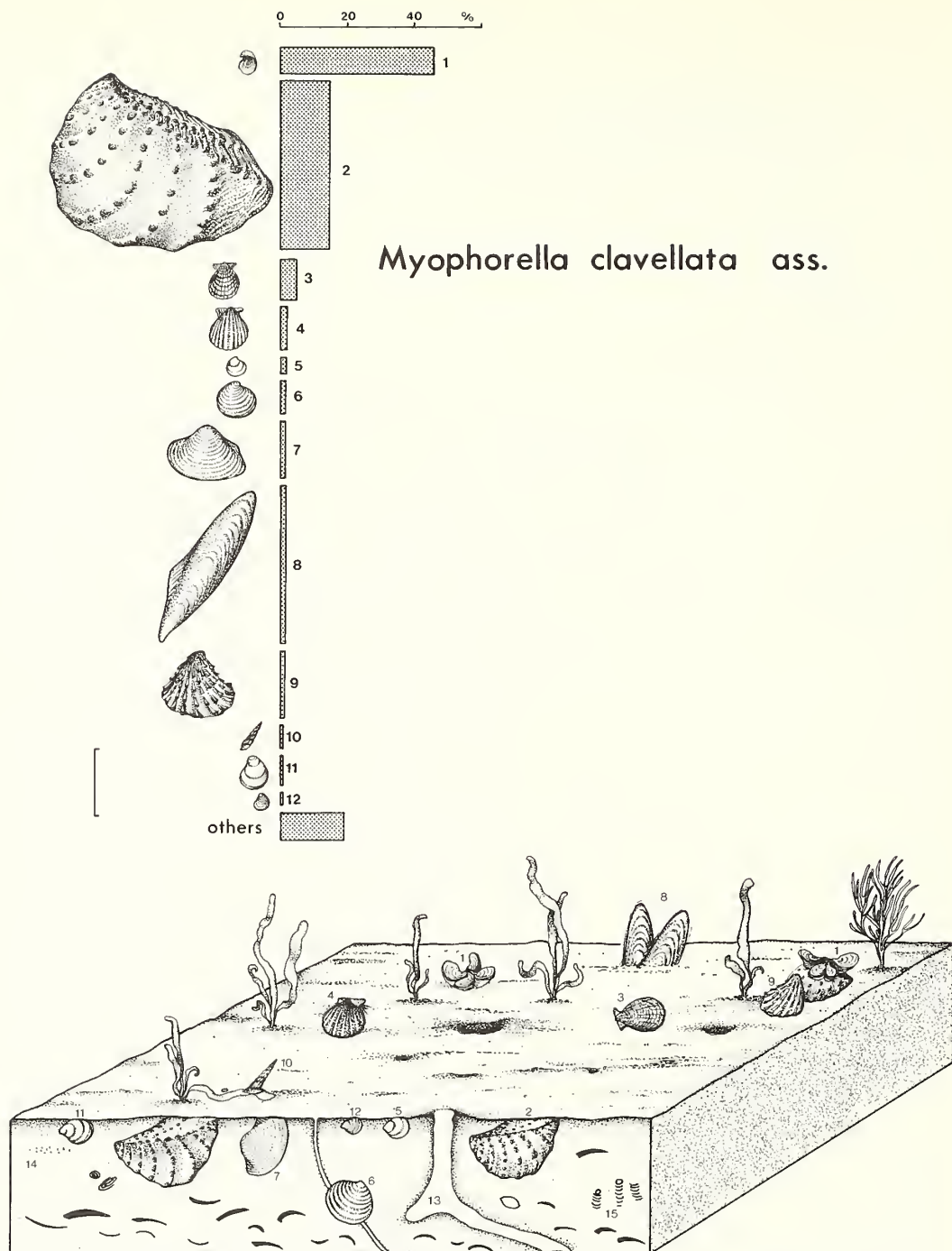


TEXT-FIG. 9. Trophic nucleus and attempted reconstruction of the *Neocrassina subdepressa* association (C). Length of bar, 6 cm. 1, *Neocrassina subdepressa*; 2, *Nanogyra nana*; 3, *Nerinella* sp.; 4, *Gervillella aviculoides*.

Discussion. There existed some doubts on the validity of this association. For instance, the absence of bivalved fauna or fauna in life position favours an origin through transportation rather than an *in situ* accumulation. On the other hand, the specimens of *N. subdepressa* exhibit a considerable size range and no signs of wear could be detected. Thus, an *in situ* origin of the association is favoured, assuming that *N. subdepressa* lived as a very shallow burrower in the muddy oolite in which it is preserved. Disarticulation and encrustation probably took place after currents excavated the infauna and the shells rested on the sea floor for some time. Association C forms a homogeneous trophic group consisting solely of suspension-feeders. Only two feeding levels can be recognized: the dominating low level suspension-feeders (e.g. *Neocrassina*) and medium level suspension-feeders (e.g. *Gervillella*).

D. *Myophorella clavellata* association

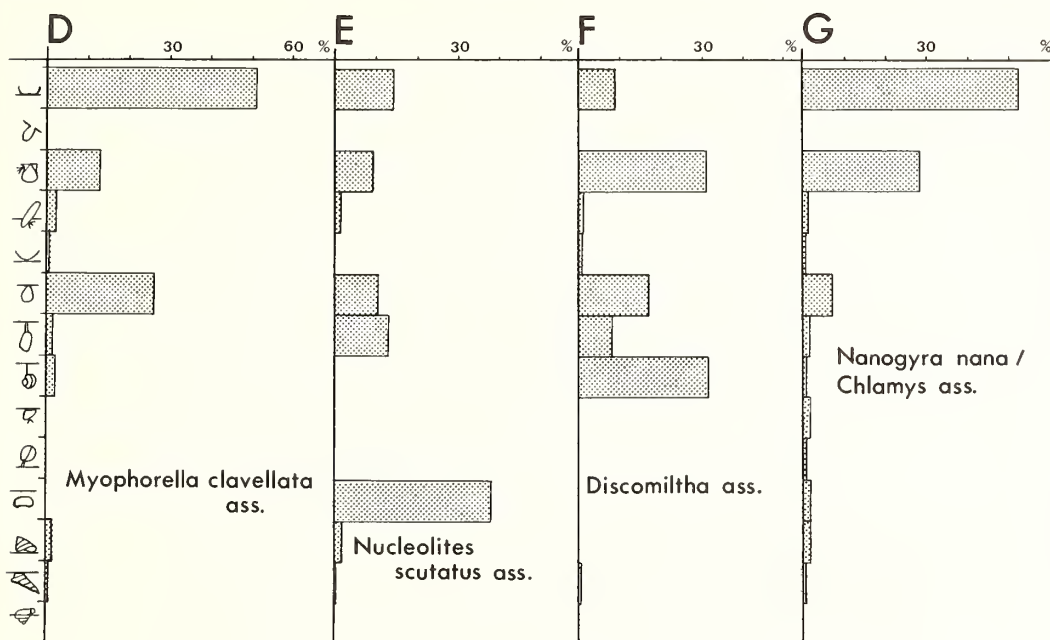
Description. The *M. clavellata* association is represented by eleven collections with 2120 species. The trophic nucleus (text-fig. 10) consists of twelve species: *Nanogyra nana* is the dominant species, followed by the shallow burrower *M. clavellata*, the epifaunal byssally attached *Chlamys* (R.) *superfibrosa* and *C. (Chl.) qualicosta*. The remainder is taken up by *Trautscholdia morini*, *Discomiltha rotundata*, *Cucullaea contracta*, *Gervillella aviculoides*, *Plicatula weymouthiana*, *Procerithium* sp., *Trautscholdia* cf. *curvirostra*, and *T. contejeani*. The association is characterized by the occurrence of several species of *Trautscholdia*, the presence of *C. contracta* and the abundance of *M. clavellata* and *Chlamys* (R.) *superfibrosa*. The latter has a second peak in its distribution in association G, but occurs there with a different set of species.



TEXT-FIG. 10. Trophic nucleus and attempted reconstruction of the *Myophorella clavellata* association (D). Length of bar, 4 cm. 1, *Nanogyra nana*; 2, *Myophorella clavellata*; 3, *Chlamys superfibrosa*; 4, *Chlamys qualicosta*; 5, *Trautscholdia morini*; 6, *Discomiltha rotundata*; 7, *Cucullaea contracta*; 8, *Gervillella aviculoides*; 9, *Plicatula weymouthiana*; 10, *Procerithium* sp.; 11, *Trautscholdia curvirostra*; 12, *Trautscholdia contejeani*; 13, *Spongiomorpha suevica*; 14, *Chondrites* sp.; 15, *Teichichnus rectus*; benthic algae hypothetical.

Bivalves form 96.9% of the fauna, followed by gastropods (2.7%), and echinoderms (0.4%). Trace fossils show a relatively high diversity (six species) and a medium abundance. The dominant forms are decapod crustacean burrows (*Spongiomorpha suevica* var. B), and burrows of various worm-shaped animals (*Chondrites*, *Teichichnus rectus*, and *Planolites*). The over-all diversity is high (text-fig. 3).

In the *M. clavellata* association epifaunal cemented bivalves (50.8%; mainly *Nanogyra*), byssally attached epifaunal bivalves (11.4%; e.g. *Chlamys*), and shallow burrowers (29.0%; e.g. the bivalves *Myophorella*, *Trautscholdia*) form the dominant ecological groups, whilst mucus-tube feeders (*Discomiltha*), semi-infaunal bivalves (*Gervillella*), and deep-burrowing bivalves (*Pholadomya*, *Pleuromya*) are of only little importance (text-fig. 11). No specimens occur in life position, but 6.6% of the bivalved fauna are preserved



TEXT-FIG. 11. Ecological composition of associations D-G. Legend in text-fig. 6.

with both valves. 8.5% of the fauna have been encrusted by *Nanogyra*, *Plicatula*, *Serpula* (*Cycloserpula*), *S. (Pentaserpula)* and the foraminifera *Nubeculinella*. 0.8% of the shells have been bored by cirripeds, polychaetes, and phoronids. Fairly common are browsing traces of echinoderms on *Chlamys* and other shells. Fragmentation ranges from 50 to 95%, with a mean value of 90%. Shell orientation has been measured in seven collections (Table 2). All but one sample showed a clear dominance of shells in the convex-up position. In two cases imbrication could be found. 15.4% of the fauna (mainly shallow- and deep-burrowing bivalves as well as many gastropods) are preserved as steinkerns. In some collections a large number of the specimens are worn or exhibit algal envelopes.

The *M. clavellata* association occurs in Normandy and Dorset, especially in condensed sandy and/or intraclastic sideritic limestones as well as in sandy limestones and marls, thus showing a clear substrate preference.

Discussion. The *M. clavellata* association occurs in two modifications: the collections from Normandy are of low diversity, show considerably better preservation, are less encrusted and bored, and less fragmented, whilst the Dorset collections exhibit a high diversity, often a bad preservation (algal envelopes, signs of wear), and a higher percentage of the fauna is fragmented and bored. In Dorset, high density

TABLE 2. Shell orientation in the *Myophorella clavellata* association (D).

Collection	Convex-up	Convex-down	Oblique
BR 44	100	15	19
BR 47	100	33	47
BH 24	100	25	33
BH 28 top	100	38	21
SC 16	100	28	79*
HV I 15	18	54	58*
HV II 5	71	11	8

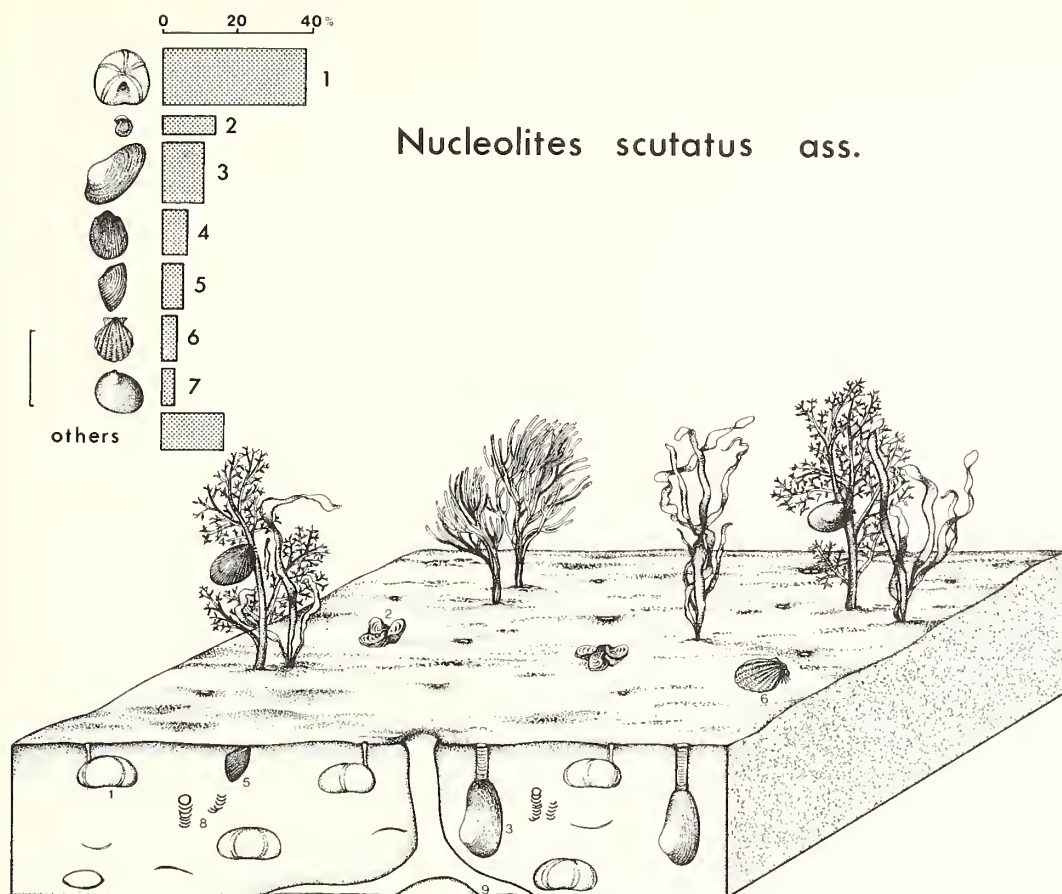
* Shells partially imbricated.

of the fauna, bad preservation, and the mixed and sideritic substrate point to a slow accumulation resulting in, at least partially, condensed deposits. Extensive lateral transport of the fauna seems unlikely as no size sorting exists and some shells are excellently preserved and sometimes bivalved. A parautochthonous accumulation caused by excavation and short, small-scale transport of the shells by currents seems a more feasible model for the formation of this association. The *Myophorella* association of Dorset cannot therefore be regarded as the remnant of one ancient community but components from several neighbouring communities probably contributed to its composition. Very likely not only horizontal but also vertical mixing took place: the high diversity of the fauna (indicated especially by the large number of species in the trophic nucleus) suggests that a change in community took place once or several times during the accumulation of the beds. Despite the fact that faunal mixing played a certain role in the collections from Dorset, they nevertheless represent a very distinct association. Only the *Neocrassina subdepressa* association (C) exhibits a similar ecological structure (compare text-figs. 6 and 11), but there the infauna consists of different elements (*Neocrassina* instead of *Myophorella* and *Trautscholdia*) and the cemented epifauna plays a far lesser role. That a *Myophorella* community existed at some time in the Upper Jurassic of north-west Europe, can also be demonstrated with most of the collections from Normandy which also show signs of short-stage transport but occur in beds which indicate normal or even rapid sedimentation.

Two trophic groups are present in the *Myophorella* association: 96.7% of the fauna are suspension-feeders, whilst 3.3% are deposit-feeders (mucus-tube-feeding *Discomiltha* and *Procerithium*). Four feeding levels can be distinguished: the very rare *Palaeonucula* as well as the trace fossils *Teichichnus*, *Cylindrichnus*, and *Chondrites* representing the infaunal deposit-feeders, *Discomiltha* and *Procerithium* deposit-feeders at the depositional interface, the common *Myophorella* and *Trautscholdia* the low level suspension-feeders, and *Gervillella* the medium level suspension-feeders.

E. *Nucleolites scutatus* association

Description. Seven hundred and eighty-six specimens in six collections represent this association. The trophic nucleus consists of seven species (text-fig. 12), the most important being the echinoid *N. scutatus*, followed by *Nanogyra nana*, *Pleuromya uniformis*, *Meleagrinella ovalis*, *Sowerbya triangularis*, *Chlamys*



TEXT-FIG. 12. Trophic nucleus and attempted reconstruction of the *Nucleolites scutatus* association (E). Length of bar, 4 cm. 1, *Nucleolites scutatus*; 2, *Nanogyra nana*; 3, *Pleuromya uniformis*; 4, *Meleagrinella ovalis*; 5, *Sowerbya triangularis*; 6, *Chlamys fibrosa*; 7, *Meleagrinella laevis*; 8, *Teichichnus rectus*; 9, *Spongiomorpha suevica*; benthic algae and hydrozoan/anthozoan coelenterate hypothetical.

(*R.*) *fibrosa*, and *M. laevis*. The association is characterized by *Nucleolites scutatus* and *M. ovalis*; in addition, *S. triangularis* reaches here the peak of its distribution. Bivalves (58.9%) no longer form the only important group of the fauna, but echinoderms (38.5%) are of nearly equal importance. Gastropods (2.5%) only play a minor role. The *N. scutatus* association is dominated by infaunal elements (text-fig. 11); the echinoids *Nucleolites*, *Clypeus*, and *Holactypus*, shallow-burrowing bivalves like *Sowerbya* and *Anisocardia*, deep-burrowing *Pleuromya*, and infaunal gastropods like *Pseudomelania* constitute 62.8% of the fauna. Byssally attached epifaunal elements (34.3%) are not so much represented by the genus *Chlamys* (as is the case in most other associations) but by the free-swinging pendant *Meleagrinella*. The number of epifaunal cemented forms is relatively low (14.4%). Trace fossils are of medium abundance and diversity; the ichnospecies present are: *Spongiomorpha suevica* var. B, *Teichichnus rectus*, *Skolithos* sp., and the resting trace of an anthozoan (*Bergaueria* sp.), i.e. a mixture between deposit-feeders, suspension-feeders, domichnia, fodinichnia, and cubichnia. The over-all diversity is medium (text-fig. 3). Only 0.6% of the uncemented fauna occur in life position (mainly *Homomya*, *Pleuromya*), but 22.5% of the bivalved fauna are preserved with both valves (amongst them epifaunal forms like *Meleagrinella*). *Dorsoserpula*, *Cyclo-serpula*, *Nanogyra*, and the bryozoan *Berenicea* encrust 3.7% of the fauna; boring elements are not present.

Fragmentation ranges from 0 to 95%, the mean value is around 60%. Except for 9.9% (mainly deep-burrowing bivalves and some gastropods which occur as steinkerns) the specimens are preserved with their shell. In two collections, a part of the epifauna exhibits algal envelopes; otherwise no signs of wear have been found.

The *Nucleolites scutatus* association shows a substrate preference for limestones which may, however, range from pure micritic limestones to oolites. Sandy, somewhat shelly limestones dominate.

Discussion. The *N. scutatus* association can be regarded as the autochthonous relic of an ancient community. This is stressed by the high percentage of bivalves preserved with both valves. That no fauna in life position has been found might be due to the fact that in the case of the burrowing echinoderm *Nucleolites* life position and stable position are identical (thus quite a few of the *Nucleolites* might be preserved in life position). The two collections, in which part of the epifauna is encrusted by calcareous algae and other organisms, have been found in shelly limestone and poorly sorted oolite. There, a relatively high energy level probably led to discontinuous sedimentation and *in situ* reworking which remained restricted to the epifauna. The other collections represent quieter environments with continuous sedimentation which is indicated by the excellent preservation of the fauna (in addition, many *Nucleolites* are filled with calcite and not with sediment). Both, deposit-feeders (*Nucleolites*) and suspension-feeders (the remaining fauna), are present in the association and lead to an inhomogeneous trophic grouping. Four feeding levels may be recognized: infaunal deposit-feeders (*Nucleolites*, *Teichichmus*), low-level suspension-feeders (e.g. *Pleuromya*, *Anisocardia*, *Nanogyra*), medium-level suspension-feeders (*Gervillella*), and high-level suspension-feeders (pendent *Meleagrinella*). The low number of epifaunal encrusting bivalves is clearly related to the low percentage of other epifauna which restricted the substrate suitable for colonization.

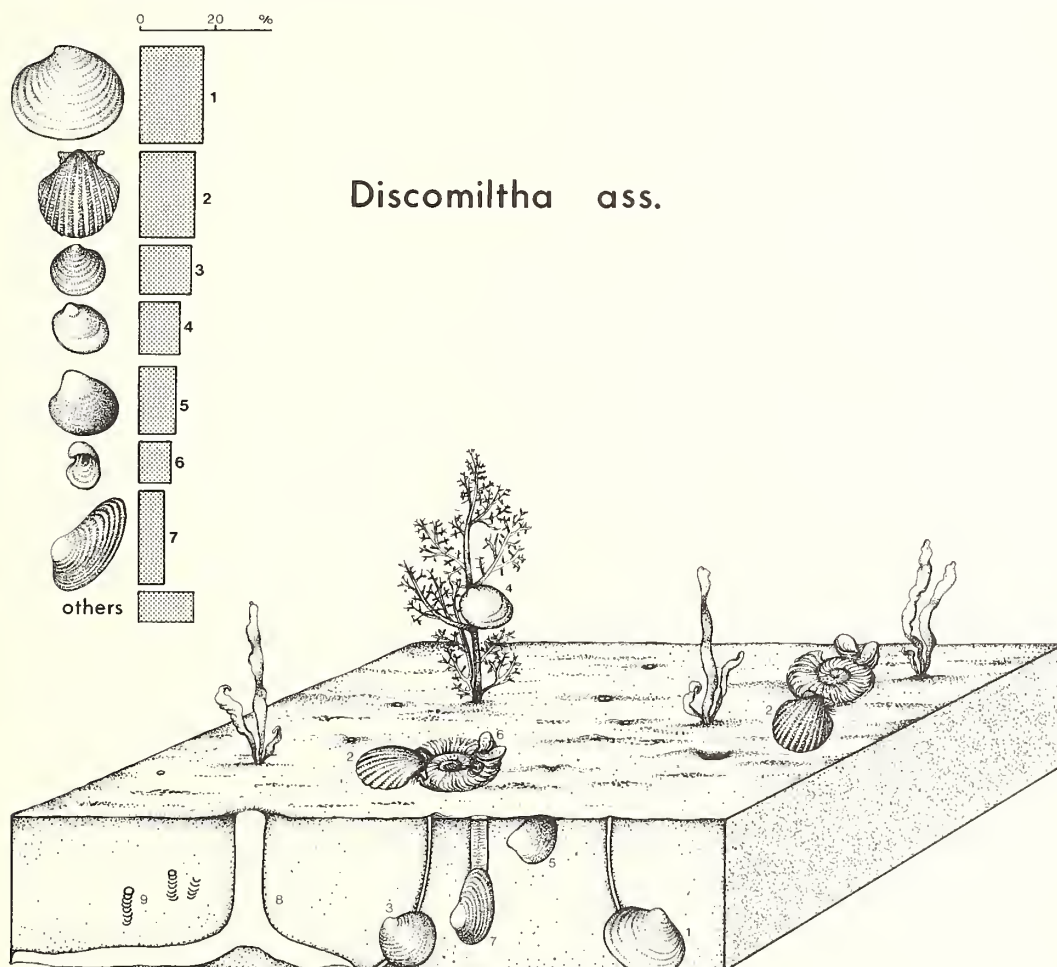
F. *Discomiltha* association

Description. The *Discomiltha* association is only represented by two collections with 702 specimens. The trophic nucleus (text-fig. 13) contains two species of *Discomiltha*, *D. lirata*, and *D. rotundata*, the remaining species being *Chlamys* (*R.*) *midas*, *Meleagrinella laevis*, *Anisocardia isocardioides*, *Nanogyra nana*, and *Pleuromya uniformis*. Four of these species are characteristic of the association: *D. lirata*, *D. rotundata*, *A. isocardioides*, and *M. laevis*. *C. midas* reaches a second peak in its distribution in the *Pinna* association and is thus less specific. As usual, bivalves dominate the fauna (99.6%) with gastropods forming the rest. Ammonites (not discussed here) are a very common faunal element. Trace fossils are of low diversity but high abundance and consist of the crustacean burrows *Spongiomorpha suevica* var. B, *Sp. paradoxa*, and of *Teichichmus*. The over-all diversity is relatively low (text-fig. 3). Ecologically, mucus-tube feeders (*Discomiltha*) and epifaunal byssally attached bivalves (e.g. *Chlamys*, *Meleagrinella*) are of equal importance (31.8% and 31.0% respectively; see text-fig. 11). Shallow burrowers (8.1%; e.g. *Pleuromya*) and epifaunal cemented forms (9.2%; *Nanogyra*) comprise the rest. No specimens were found in life position, but 25.5% of the bivalves (predominantly *Discomiltha* and *Pleuromya*) are preserved with both valves. 1.4% of the fauna are encrusted by *Cycloserpula*; no specimens are bored. Fragmentation is in both collections about 50%. Nearly four-fifths of the specimens, mainly the burrowing bivalve fauna and the ammonites, are preserved as steinkerns.

Both collections are from medium-grained sandstone which indicates the narrow facies and substrate range of association F.

Discussion. The *Discomiltha* association is the relic of an ancient community which is indicated by the high percentage of specimens preserved with both valves and the low percentage of fragmented forms. The extensive burrow systems of crustaceans (*Spongiomorpha*) point to fairly stable conditions at least for part of the time.

Their producers (deposit-/suspension-feeders or scavengers?) constituted an important part of the community. The absence of infaunal deposit-feeding bivalves is probably due to the relatively coarse substrate, whilst the encrusting fauna lacked substrate suitable for colonization and is thus far below its usual significance. No other association possesses a similar ecological structure. The occurrence of two species of *Discomiltha* among three most common representatives of the trophic nucleus indicates that interspecific competition must have been low, or else, that small differences in the feeding habit existed. Five feeding levels can be distinguished: infaunal deposit-feeders (represented by *Teichichnus*), deposit-feeders at the depositional interface (*Discomiltha*), low-level suspension-feeders (e.g. *Chlamys*, *Pleuromya*, *Anisocardia*), medium-level suspension-feeders, represented by some *Pinna* and

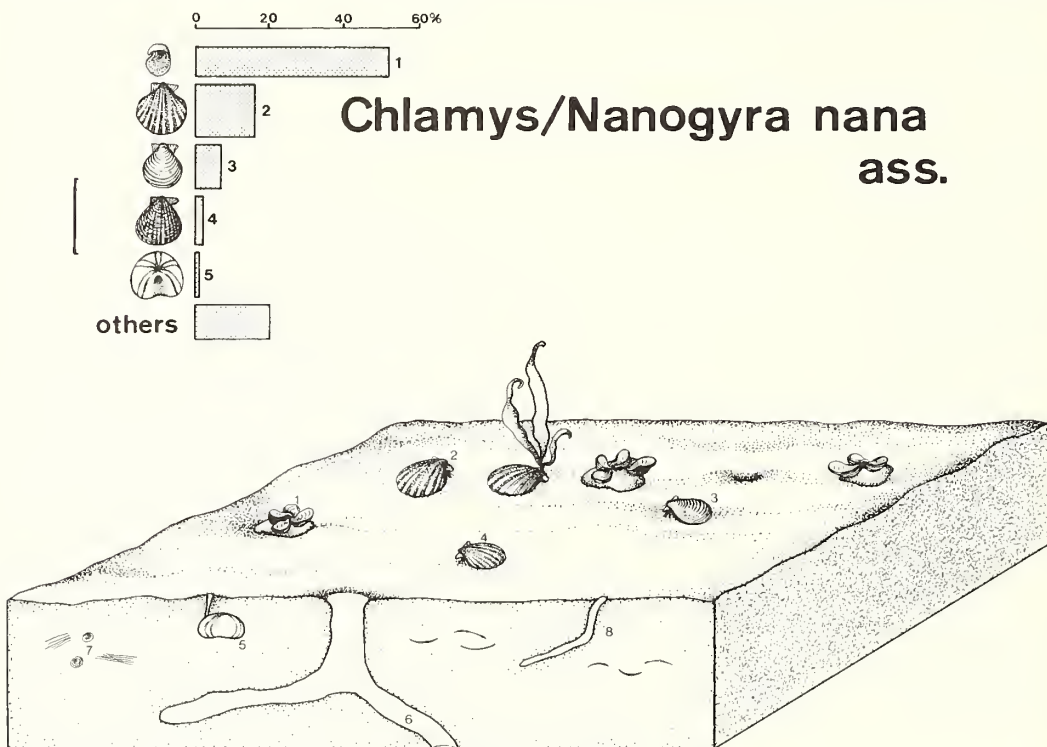


TEXT-FIG. 13. Trophic nucleus and attempted reconstruction of the *Discomiltha* association (F). Length of bar, 3 cm. 1, *Discomiltha lirata*; 2, *Chlamys midas*; 3, *Discomiltha rotundata*; 4, *Meleagrinella laevis*; 5, *Anisocardia isocardioides*; 6, *Nanogyra nana*; 7, *Pleuromya uniformis*; 8, *Spongiomorpha suevica*; 9, *Teichichnus rectus*; benthic algae and hydrozoan/anthozoan coelenterate hypothetical.

Gervillella, and high-level suspension-feeders (e.g. the pendent *Meleagrinella*). The numerous vagile ammonites (mainly *Amoeboceras*, less common perisphinctids) most likely formed a third trophic group, namely scavengers (Lehmann 1975) or predators.

G. *Chlamys/Nanogyra nana* association

Description. Eighteen collections with 2908 specimens have been grouped into this association. *N. nana* is with 52.1% the dominant species (text-fig. 14) followed by *C. (R.) fibrosa*, *C. (R.) superfibrosa*, and



TEXT-FIG. 14. Trophic nucleus and attempted reconstruction of the *Chlamys/Nanogyra nana* association (G). Length of bar, 4 cm. 1, *Nanogyra nana*; 2, *Chlamys fibrosa*; 3, *Chlamys superfibrosa*; 4, *Chlamys qualicosta*; 5, *Nucleolites scutatus*; 6, *Spongiomorpha suevica*; 7, *Cylindrichnus concentricus*; 8, *Planolites* sp.; benthic algae hypothetical.

C. (C.) qualicosta. The burrowing echinoid *Nucleolites scutatus* and the shallow-burrowing bivalve *Sowerbya triangularis* complete the trophic nucleus. The association is characterized by the dominance of pectinids and of *Nanogyra*. Bivalves comprise 93.8% of the fauna, gastropods 3.2%, echinoderms 1.7%, brachiopods 0.3%, and free-living serpulids 0.2%. The epifauna (86.1%; text-fig. 11) consists mainly of cemented *Nanogyra* and byssally attached pectinids, the infauna (12.6%) predominantly of shallow burrowers like *Sowerbya*, *Trautscholdia*, and *Isocyprina*. Infaunal gastropods, *Nucleolites*, and deep-burrowing bivalves are of lesser significance as are semi-infaunal animals (*Gervillella*, *Pinna*). For the first time, deposit-feeding nuculids (1.1%) occur in an association more than just as scattered individuals. Trace fossils show a very high diversity (eight species) and medium abundance. The dominant ichnospecies are *Spongiomorpha suevica* var. B, *Planolites* sp., and the burrow of a worm-shaped animal, *Cylindrichnus concentricus*. The over-all diversity is high (text-fig. 3). No species occur in life position except *Nanogyra* and other

cemented forms and the percentage of specimens preserved with both valves is low (2·9%). 5% of the fauna are encrusted by various serpulids (*Cycloserpula*, *Dorsoserpula*, *Pentaserpula*), the bivalves *Nanogyra* and *Placunopsis*, bryozoans, and the foraminifera *Nubeculinella*. *Lithophaga inchoa* and cirripedes account for the few bored specimens (0·1%). Fragmentation varies between 30 and 98% and is usually around 90%. Orientation of shells could be measured in one collection; convex-up shells dominated (convex-up: convex-down = 100:65; oblique: 41). 5·3% of the fauna, predominantly burrowing forms (*Pleuromya*, *Palaeonucula*, *Protocardia*) more rarely epifaunal elements, are preserved as steinkerns. Only rarely do specimens exhibit signs of wear but commonly show algal envelopes when found in oolites or bioclastic limestones.

The *Chlamys/N. nana* association occurs in a wide range of substrates and facies types, in clays as well as in oolites whereby a certain preference for sandstones and impure limestones was noted. In several collections bored and encrusted pebbles are associated with the fauna.

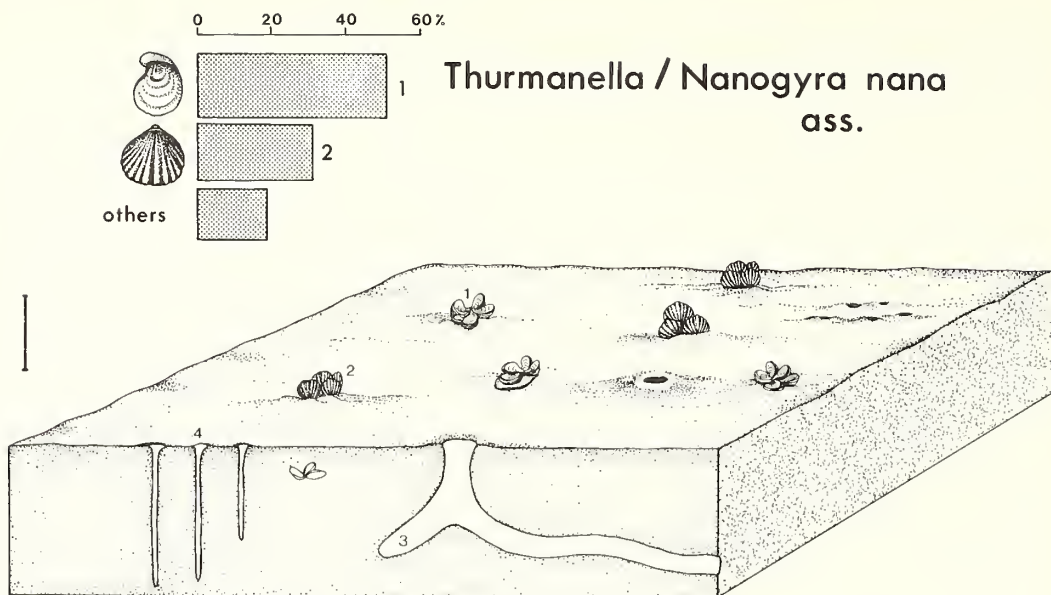
Discussion. The *Chlamys/N. nana* association is one of the commonest associations in the Corallian, found from Normandy all the way to the Yorkshire coast. Although its characteristic members can also be found in nearly all other associations, it is here that they reach the peak of their distribution (*Nanogyra* excepted). The environment in which this association accumulated was quite varied, judging from its wide range of facies, but a fairly high energy level is probable for most samples. Reworking was a common feature (encrusted and bored pebbles, high fragmentation rate, algal envelopes) and some species like *Lopha genuiflecta* reacted in developing occasionally extremely thick and heavy shells. The percentage of still bivalved specimens is insignificant and no forms are preserved in life position. The substrate was of little attraction for the infauna as the cemented and byssally attached epifauna is the dominating faunal element. *Nanogyra* growing on dead shells formed little clusters on the sea floor and the pectinids similarly may have used shell material for fixation of their byssus.

Apart from this high-energy variety, a few collections seem to be derived from a low-energy environment represented by clays and silts. There, the fauna is better preserved and the infauna is of greater abundance and diversity with some deposit-feeding *Procerithium*, *Discomiltha*, and *Palaeonucula* occurring besides infaunal suspension-feeders (*Pseudomelania*).

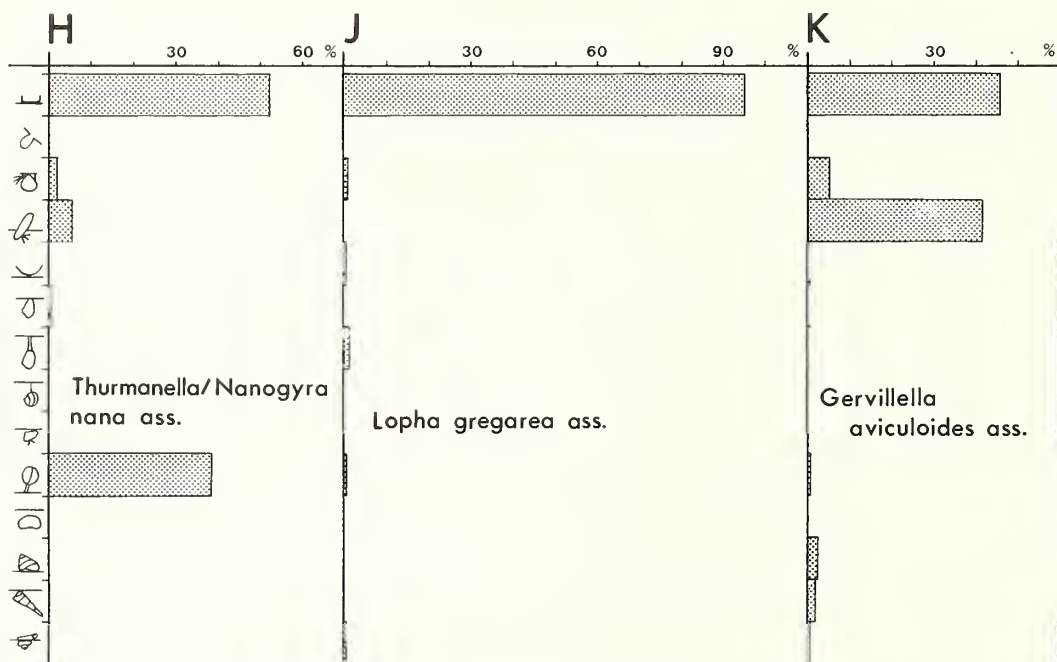
The *Chlamys/N. nana* association has a similar ecological composition to the oyster/*Isognomon promytiloides* association (compare text-figs. 11 and 21) but there *Chlamys* is replaced by *Isognomon* and *Nanogyra* has to compete with *Plicatula* and other oysters. Two trophic groups (deposit-feeders, suspension-feeders) are present in association G and three feeding levels can be recognized: infaunal deposit-feeders (*Palaeonucula*), low-level suspension-feeders (*Chlamys*, *Pleuromya*, *Sowerbya*), and medium-level suspension-feeders (*Gervillella*, *Pinna*).

H. *Thurmanella acuticosta*/*Nanogyra nana* association

Description. Three collections with 921 specimens form this association which has been encountered only in Yorkshire. The trophic nucleus (text-fig. 15) consists of two species, the bivalve *N. nana* and the brachiopod *Thurmanella acuticosta*. *Gervillella aviculoides* and a species of 'Terebratulid' are two further common faunal elements. The association is characterized by the high percentage of rhynchonellid or terebratulid brachiopods which otherwise are a rare faunal element. Hardly any infauna is present (0·9%), but epifaunal cemented bivalves (52·5%), pedicle-attached brachiopods (38·5%) and, to lesser extent, epifaunal byssally attached bivalves (2·0%; mainly *Chlamys*) prevail (text-fig. 16). With 5·8%, the semi-faunal bivalves (*Gervillella*, *Pinna*) are relatively well represented. Long stems of the crinoid *Millericrinus* are commonly found on the bedding planes; starfish ossicles abound in the sediment. Trace fossils (*Spongiomorpha suevica* var. B and *Skolithos*) are of low diversity and medium abundance. The over-all diversity is similarly



TEXT-FIG. 15. Trophic nucleus and attempted reconstruction of the *Thurmanella acuticosta*/*Nanogyra nana* association (H). Length of bar, 2 cm. 1, *Nanogyra nana*; 2, *Thurmanella* sp.; 3, *Spongiomorpha suevica*; 4, *Skolithos* sp.



TEXT-FIG. 16. Ecological composition of associations H-K. Legend in text-fig. 6.

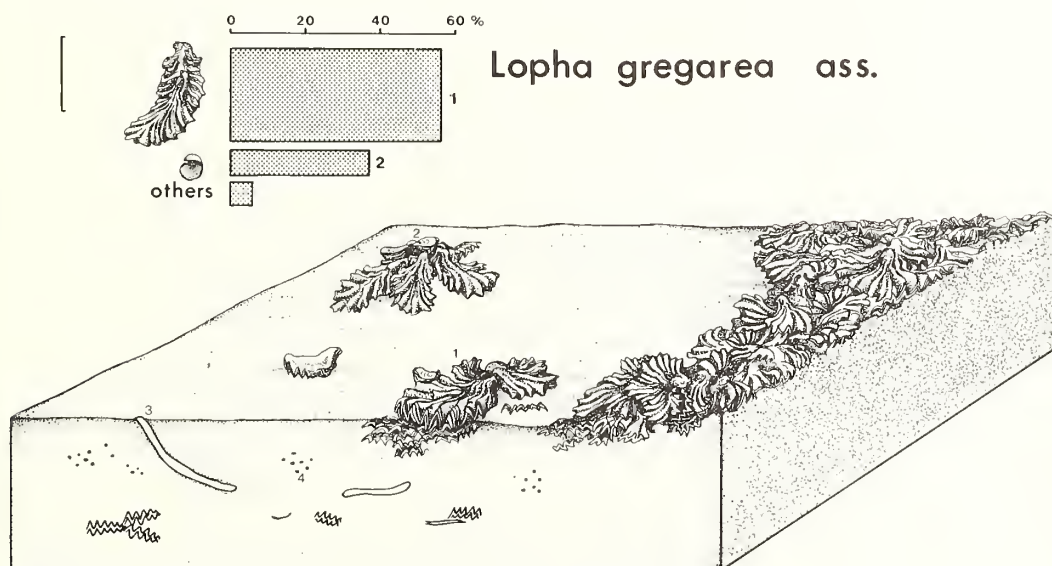
very low (text-fig. 3). Of the uncemented fauna 57.6%, mainly *Thurmanella* and '*Terebratula*', occur in life position as do most cemented *Nanogyra*, and 39% of the specimens are still bivalved. Only a few specimens are encrusted with the bryozoan *Berenicea* or with *Nanogyra*, even less are bored by polychaetes. Fragmentation ranges from 65 to 75%. All faunal elements are preserved with their shells.

The three collections show a distinct substrate preference occurring in oolitic/sandy limestones and oolitic calcareous sandstones.

Discussion. As only thick-shelled aragonitic burrowers are preserved (*Myophorella*), some preservational bias cannot be excluded, with the thin-shelled species dissolved during diagenesis. Apart from this, the *Thurmanella*/*Nanogyra* association is the remnant of an ancient community. This can be inferred from the high percentage of fossils still bivalved and in life position. Hardly any transport has been involved: *Nanogyra* and the brachiopods are found as small clusters with calcite or geopetal fills dispersed on the bedding plane as they were originally on the sea floor. Partly articulated *Millericrinus* also indicate that the fauna is autochthonous. The low percentage of bored and encrusted shells indicates continuous sedimentation; the substrate and faunal composition suggest moderate currents. Deposit-feeders are not represented, but the abundant starfish ossicles indicate that algal grazing, scavenging, or predatory starfish played an important role in the ecosystem. Three feeding levels can be distinguished: infaunal deposit-feeders (crustaceans) low-level suspension-feeders (e.g. the producer (worms, phoronids?) of *Skolithos*, *Myophorella*, *Nanogyra*, brachiopods), medium-level suspension-feeders (*Gervillella*, *Pinna*), and high-level suspension-feeders (*Millericrinus*).

J. *Lopha gregarea* association

Description. The *L. gregarea* association is represented by 616 specimens in six collections. The trophic nucleus (text-fig. 17) consists of two epifaunal cemented bivalves: *L. gregarea* and *N. nana*. The association



TEXT-FIG. 17. Trophic nucleus and attempted reconstruction of the *Lopha gregarea* association (J). Length of bar, 4 cm. 1, *Lopha gregarea*; 2, *Nanogyra nana*; 3, *Planolites* sp.; 4, *Chondrites* sp.

is characterized by *L. gregarea* which reaches here the peak of its distribution. Bivalves (98.5%) dominate the association with serpulids (0.8%) and brachiopods (0.6%) forming the rest, whilst gastropods are missing. Trace fossils are of low abundance and diversity; they are represented by *Chondrites* and pyritic tubes. The over-all diversity is very low (text-fig. 3). Except for a few epifaunal byssally attached bivalves (1.0%) and deep-burrowing bivalves (1.3%) the fauna is dominated by cemented bivalves (95.3%; see text-fig. 16). No uncemented forms are preserved in life position but the majority of *Lopha* and *Nanogyra* occur in life position forming low biostromes. 11.6% of the specimens are still bivalved. Due to the predominance of epifauna, 57.6% of the fauna are encrusted by *Nanogyra*, the foraminifera *Nubeculinella*, the bryozoans *Berenicea* and *Stomatopora*, and various serpulids (*Cycloserpula*, *Dorsoserpula*, and *Pentaserpula*). 4% of the fauna are bored; the animals responsible being the bivalve *Lithophaga inclusa* and a phoronid. Fragmentation varies between 75 and 90%. Most specimens are preserved with their shell intact except some deep-burrowing *Pholadomya* which occur in steinkern preservation.

Discussion. Only present in Normandy, the *Lopha gregarea* association exhibits a similar ecological composition as the *Nanogyra* association (R), but there *Lopha* is replaced by *Nanogyra* which is the only dominant faunal element. The environment is very similar to that of association A (see p. 347), i.e. relatively low rates of sedimentation and only interludes of high-energy conditions. This led to a stable substrate upon which extensive oyster beds grew up to 20 cm high. These beds could be followed laterally for several hundred metres. The dense mass of *L. gregarea* provided in turn an ecological niche for smaller encrusters like *Nanogyra* and the numerous serpulids. Whilst some collections represent the *in situ* *L. gregarea* community of Upper Jurassic times, in some others the shell beds have been broken up and clusters of individuals scattered on the sea floor, indicating the destruction of the community by strong currents. The fact that a large part of the sea floor was covered with these oyster beds is probably responsible for the extremely low percentage of burrowing fauna.

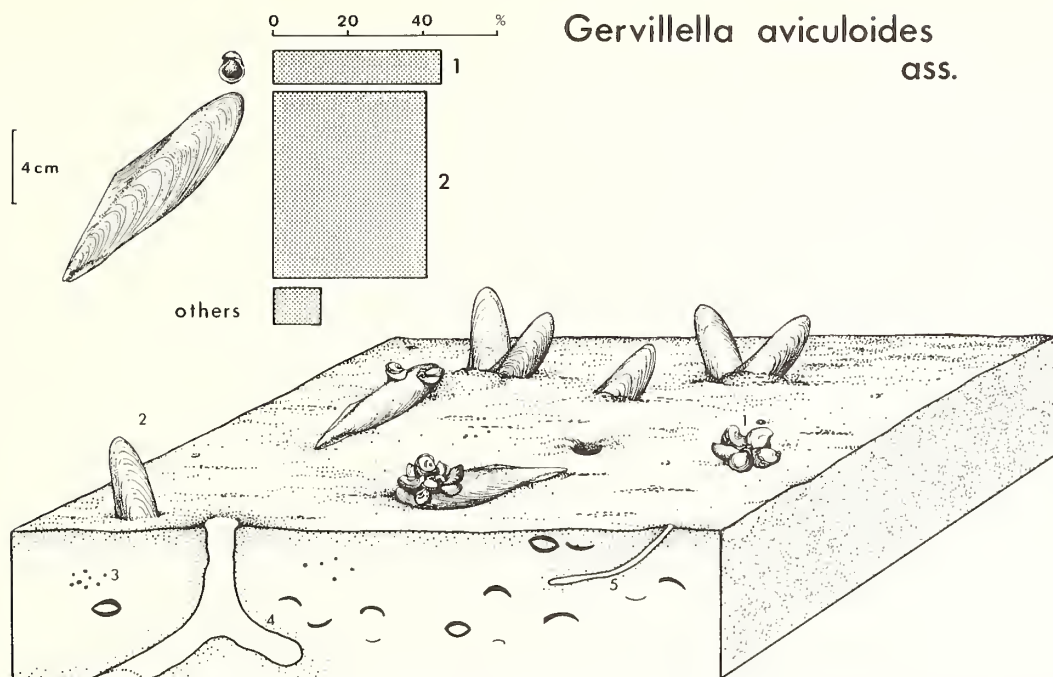
Only two feeding levels can be distinguished: infaunal deposit-feeders (sipunculoid worms?) represented by *Chondrites* and pyritic tubes, and low-level suspension-feeders (rare burrowing bivalves, *Lopha*, *Nanogyra*).

K. *Gervillella aviculoides* association

Description. Three hundred and fifty-two specimens in three collections form the *G. aviculoides* association. Its trophic nucleus (text-fig. 18) consists of the bivalves *N. nana* and semi-infaunal *G. aviculoides*. The characteristic species is *Gervillella* which reaches here the peak of its distribution. As usual, bivalves dominate the fauna (94.6%) followed by gastropods (4.3%), brachiopods (0.6%), and free-living serpulids (0.6%). The fossils are of medium diversity and abundance; the dominant ichnogenera comprise *Chondrites*, *Spongiomorpha suevica* var. B, and *Planolites*. The over-all diversity is low (text-fig. 3). Semi-infaunal bivalves (41.8%) and cemented epifauna (46.3%; e.g. *Nanogyra*) are of nearly equal importance whilst the byssally attached epifauna (5.1%; e.g. *Chlamys*), epifaunal gastropods (2.3%; e.g. *Ampullina*), and infaunal gastropods (2.0%; *Pseudomelania*) are of lesser significance (text-fig. 16). Infaunal bivalves represented solely by *Isocyprina* and *Cucullaea* are very rare. No specimens are preserved in life position, but 27.1% are still bivalved. 7.4% of the fauna is encrusted by *Nanogyra* and *Pentaserpula*, bored specimens were not encountered. Fragmentation ranges from 50 to 75%. All specimens are preserved with their shell.

The *G. aviculoides* association occurs in Yorkshire and Oxfordshire and shows a substrate preference for oolites and impure limestones.

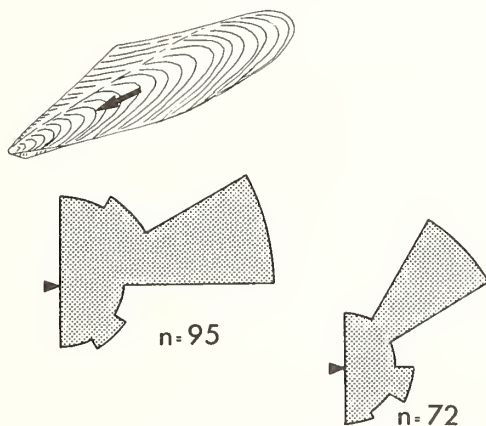
Discussion. Calcite preservation of the fauna and absence of any aragonitic burrowers point to a preservational bias of the association but as all aragonitic gastropods are preserved with their shell the absence of the burrowing bivalves seems to be genuine. Thus, the coarse substrate might have been unsuitable for burrowers. The three



TEXT-FIG. 18. Trophic nucleus and attempted reconstruction of the *Gervillella aviculoides* association (K). 1, *Nanogyra nana*; 2, *Gervillella aviculoides*; 3, *Chondrites* sp.; 4, *Spongiomorpha suevica*; 5, *Planolites* sp.

collections represent different stages of reworking of an ancient *G. aviculoides* community, ranging from a sample from the Tabular Hills (Yorkshire) where nearly all *Gervillella* are preserved with both valves to a sample from Shellingford Cross Roads Quarry, Berkshire, where most specimens are one-valved and show current orientation (text-fig. 19). But even there, the transport involved must have been minimal as the *Gervillella* range from 3.5 to 15.0 cm in size and are well preserved. Thus, the *G. aviculoides* association can be regarded as the partially reworked autochthonous relic of an ancient community which seems to have thrived in a relatively high-energy environment.

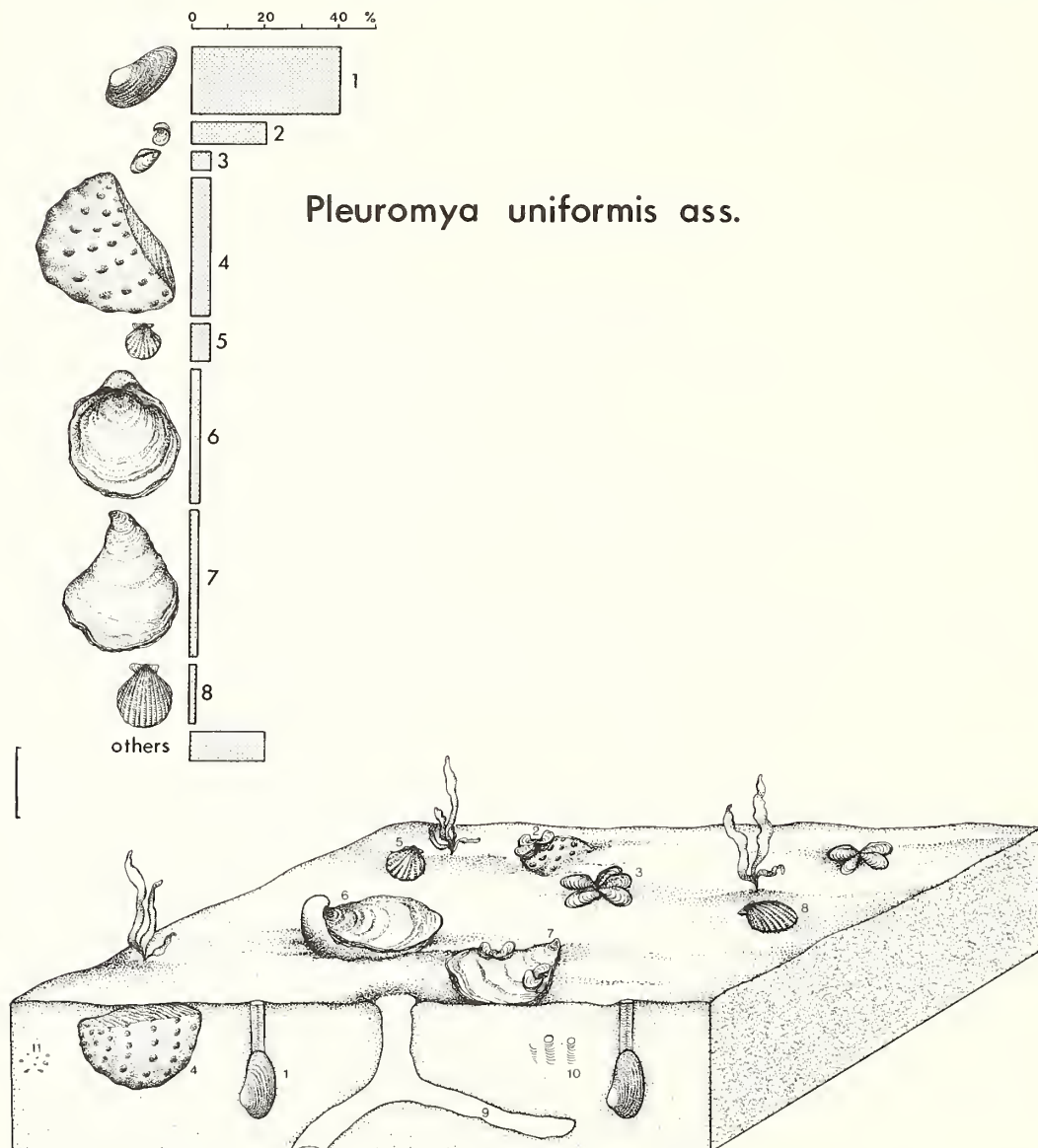
Three feeding levels can be distinguished: infaunal deposit-feeders represented by *Planolites* and *Chondrites*, low-level suspension-feeders (e.g. *Isoocyprina*, *Nanogyra*), and medium-level suspension-feeders (*Gervillella*, large *Plagiostoma*).



TEXT-FIG. 19. Orientation of flat-lying *Gervillella aviculoides* in the *Gervillella aviculoides* association. Bedding planes of fallen blocks, Osmington Oolite Group, Shellingford Cross Roads Quarry, Berkshire.

L. *Pleuromya uniformis* association

Description. The *P. uniformis* association is with twenty-eight collections and 3272 specimens the commonest of the Corallian invertebrate associations, occurring predominantly in Dorset and, to a lesser extent, in Yorkshire. The trophic nucleus (text-fig. 20) consists of eight species of bivalves. *P. uniformis* occupies the first-rank position being followed by *N. nana*, '*Mytilus*' *varians*, *Myophorella clavellata*, *Chlamys*

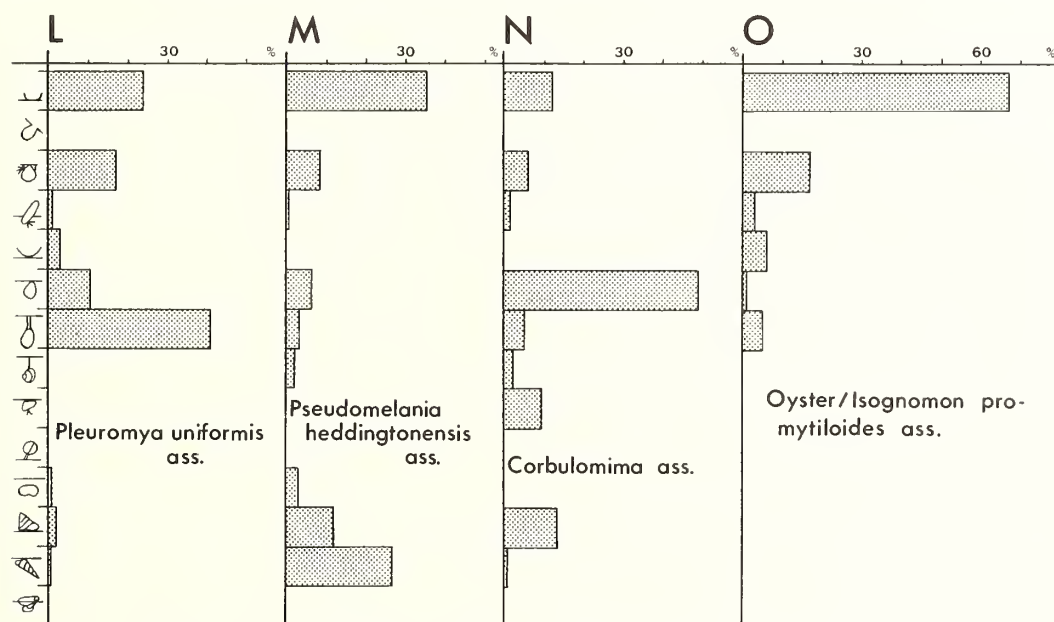


TEXT-FIG. 20. Trophic nucleus and attempted reconstruction of the *Pleuromya uniformis* association (L). Length of bar, 5 cm. 1, *Pleuromya uniformis*; 2, *Nanogyra nana*; 3, '*Mytilus*' *varians*; 4, *Myophorella clavellata*; 5, *Chlamys fibrosa*; 6, *Gryphaea dilatata*; 7, *Deltoideum delta*; 8, *Chlamys midas*; 9, *Spongehomorpha suevica*; 10, *Teichichnus rectus*; 11, *Chondrites* sp.; benthic algae hypothetical.

fibrosa, *Gryphaea* (B.) *dilatata*, *Deltoideum delta* and *C. (R.) midas*. Two species, *P. uniformis* and 'M.' *varians*, characterize the association reaching in it the peak of their distributions. As usual bivalves dominate the fauna with 96.1%; gastropods (2.6%), echinoderms (1.0%), brachiopods, serpulids, and sponges form the rest. The trace-fossil fauna is both very diverse and abundant; the more important members are *Spongeliomorpha suevica* var. B, *Chondrites*, *Teichichnus rectus*, and *Cylindrichnus concentricus*. The over-all diversity is very high (text-fig. 3). Epifauna and infauna are nearly equal in numbers (text-fig. 21), the semi-fauna represented by *Modiolus*, *Pinna*, and *Gervillella* being only of little importance (1.1%). Deep-burrowing bivalves like *Pleuromya* and *Pholadomya* (40.9%) dominate the infauna, shallow-burrowing bivalves like *Myophorella*, *Isocyprina*, and astartids account for 10.5% of the fauna; the rest is formed by the echinoid *Nucleolites*, the gastropod *Pseudomelania*, and some mucus-tube feeding bivalves (*Discomiltha*). In the epifauna, cemented bivalves (mainly *Nanogyra*) and byssally attached pectinids (*Chlamys*, *Camptonectes*) and *Isognomon* prevail. Less common are free-resting (*Gryphaea*) or swimming forms (*Entolium*) and some herbivorous or scavenging gastropods. Only 2.8% of the fauna occur in life position but 48.7% of the specimens are still preserved with both valves. The number of encrusted and bored specimens is fairly low. Epizoa are the foraminifera *Nubeculinella* and the bivalves *Nanogyra*, *Lopha*, 'Ostrea', and *Placunopsis*. *Lithophaga inclusa* and phoronids account for the borings. Fragmentation ranges from 5% to more than 95% and is usually at one end of the scale. In two collections a preferred convex-up orientation of shells larger than 2 cm has been noted, the percentage of shells in an oblique position being relatively high. A large part (39.6%) of the fauna is preserved as steinkerns, mainly the burrowing bivalves *Pleuromya*, *Pholadomya*, and *Myophorella* as well as many gastropods (especially *Ampullina* and pleurotomariids). Only rarely do specimens show signs of wear or exhibit algal envelopes.

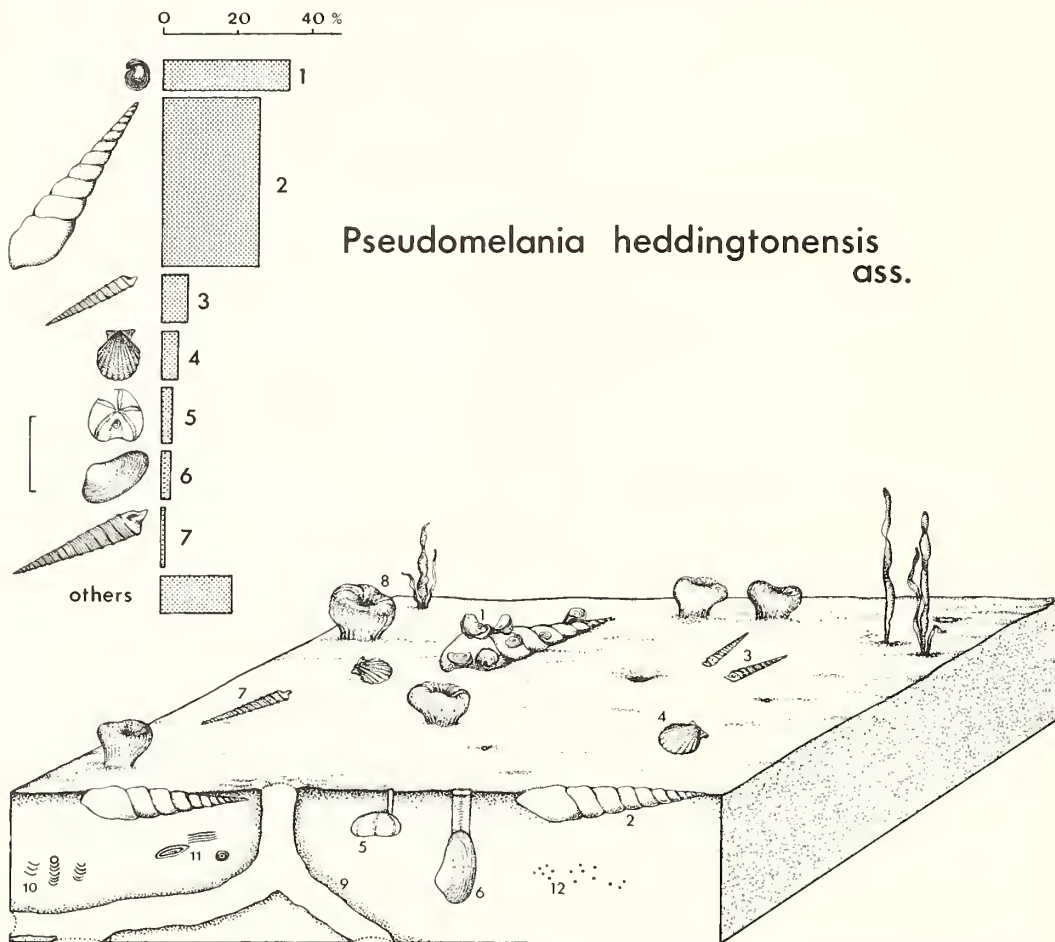
The *Pleuromya uniformis* association occurs in a very wide range of facies, from oolites to clays, but shows a preference for intraclastic, sandy limestones and fine- to medium-grained sandstones. Occasionally drift-wood and in one case bored and encrusted pebbles are associated with the fauna.

Discussion. Judging from its widespread occurrence the *P. uniformis* association thrived in a variety of environments, and seems to have dominated the offshore shelf regions where moderate currents and a somewhat reduced rate of sedimentation



TEXT-FIG. 21. Ecological composition of associations L-O. Legend in text-fig. 6.

favoured deep burrowing, as well as the even more rigorous shallow subtidal bar and nearshore environments. In some collections the composition of the fauna indicates a gradation into the condensed version of the *Myophorella* association, and the high density of the fauna, and shell beds which accumulated rather by non-deposition and only rarely by current action confirm this observation. Other collections represent a fairly true picture of the ancient *Pleuromya* community: *Pleuromya* and clusters of '*Mytilus*' *varians* (which most likely lived like the present-day *M. edulis*) in life position indicate that hardly any disturbance has taken place. In general the high percentage of bivalved specimens, the concentration of the fauna in small pockets, and the good preservation of most specimens demonstrate that transport played only a very subordinate role in the formation of the association. The low



TEXT-FIG. 22. Trophic nucleus and attempted reconstruction of the *Pseudomelania heddingtonensis* association (M). Length of bar, 4 cm. 1, *Nanogyra nana*; 2, *Pseudomelania heddingtonensis*; 3, *Nerinella* sp.; 4, *Chlamys fibrosa*; 5, *Nucleolites scutatus*; 6, *Pleuromya uniformis*; 7, *Nerinella cyane*; 8, sponge *Rhaxella* (hypothetical reconstruction); 9, *Spongiomorpha suevica*; 10, *Teichichnus rectus*; 11, *Cylindrichnus concentricus*; 12, *Chondrites* sp.; benthic algae hypothetical.

percentage of specimens in life position and, at the same time, the high percentage of bivalved fauna is in many collections probably due to the very intensive bioturbation, especially of burrowing decapods.

Three or four trophic groups are represented in the association: deposit-feeders, suspension-feeders, herbivores (e.g. *Bathrotomaria*), and possibly, scavengers (*Ampullina*?). Two feeding levels can be recognized: infaunal deposit-feeders indicated by *Planolites*, *Cylindrichnus*, *Chondrites*, and *Teichichnus*, deposit-feeders at the depositional interface (the rare *Discomiltha*) and low-level suspension-feeders (e.g. *Pleuromya*, *Myophorella*, pectinids).

M. *Pseudomelania heddingtonensis* association

Description. The *P. heddingtonensis* association is, with sixteen collections and 2194 specimens, fairly common in the Corallian. The trophic nucleus consists of seven species (text-fig. 22). *N. nana* occupies the first rank position followed by two gastropod species, *P. heddingtonensis* and *Nerinella* sp. The pectinid *Chlamys* (R.) *fibrosa*, the echinoid *Nucleolites scutatus*, the bivalve *Pleuromya uniformis* and the gastropod *Nerinella cyane* form the rest. *Pseudomelania heddingtonensis* reaches in this association the peak of its distribution and thus forms its characteristic species. Bivalves account for only 56.6% of the fauna and gastropods (39.7%) are a very important faunal element. Echinoderms (3.5%), brachiopods (0.1%), and sponges (0.04%) are of lesser significance. Trace fossils are of a high diversity and only medium abundance. The dominant forms are *Spongeliomorpha suevica* var. B, *Chondrites* sp., *Teichichnus rectus*, and *Cylindrichnus concentricus*. The over-all diversity is high (text-fig. 3). Infauna and epifauna are of nearly equal importance, the semi-fauna being hardly represented (0.6%). Amongst the epifauna (text-fig. 21), cemented bivalves form the largest group (35.5%; mainly *Nanogyra*), followed by gastropods like *Nerinella*, *Bathrotomaria*, *Coelostylina*, *Procerithium*, and *Ampullina* (13.1%), and by byssally attached bivalves (8.4%; mainly pectinids and limids). The infauna is dominated by the gastropod *Pseudomelania*. The rest consists of deep-burrowing (e.g. *Anisocardia*, *Isocyprina*) bivalves as well as echinoids (*Nucleolites*, *Pygaster*). No elements of the fauna have been found in life position except cemented bivalves; 9% of the specimens are still preserved with both valves. *Nanogyra*, *Dorsoserpula*, and the foraminifera *Nubeculinella* encrust 6% of the fauna; 0.2% are bored by the bivalve *Lithophaga inclusa* and by polychaetes. Fragmentation ranges from 20 to 98% and is usually around 90%. The thin-shelled organisms are preferredly fragmented whilst the thick shells of, for instance, *Gervillella* and *Pseudomelania* have been less affected. In seven collections orientation of shells larger than 2 cm has been measured (Table 3). The

TABLE 3. Shell orientation in the *Pseudomelania heddingtonensis* association. Only shells with a diameter larger than 2 cm have been counted. The asterisk marks collections in which imbrication has been encountered.

Collection	Convex-up	Convex-down	Oblique
P II 1b	100	12	9
*TB II 10 top	100	20	23
TB II 10 base	100	29	19
*TB II 14	100	19	28
*TB II 17	100	40	30
*TB II 18	50	13	33

overwhelming majority of the shells occurs convex-up and in four collections imbrication has been observed. 7.2% of the fauna occurs in steinkern preservation. Amongst them are many deep-burrowing bivalves, some shallow burrowers, and most gastropods except *Pseudomelania*. Occasionally shells exhibit algal envelopes, more rarely are they worn.

Discussion. The *P. heddingtonensis* association is widespread in the Malton Oolite of the Vale of Pickering, Yorkshire, but is also found in Normandy and Dorset.

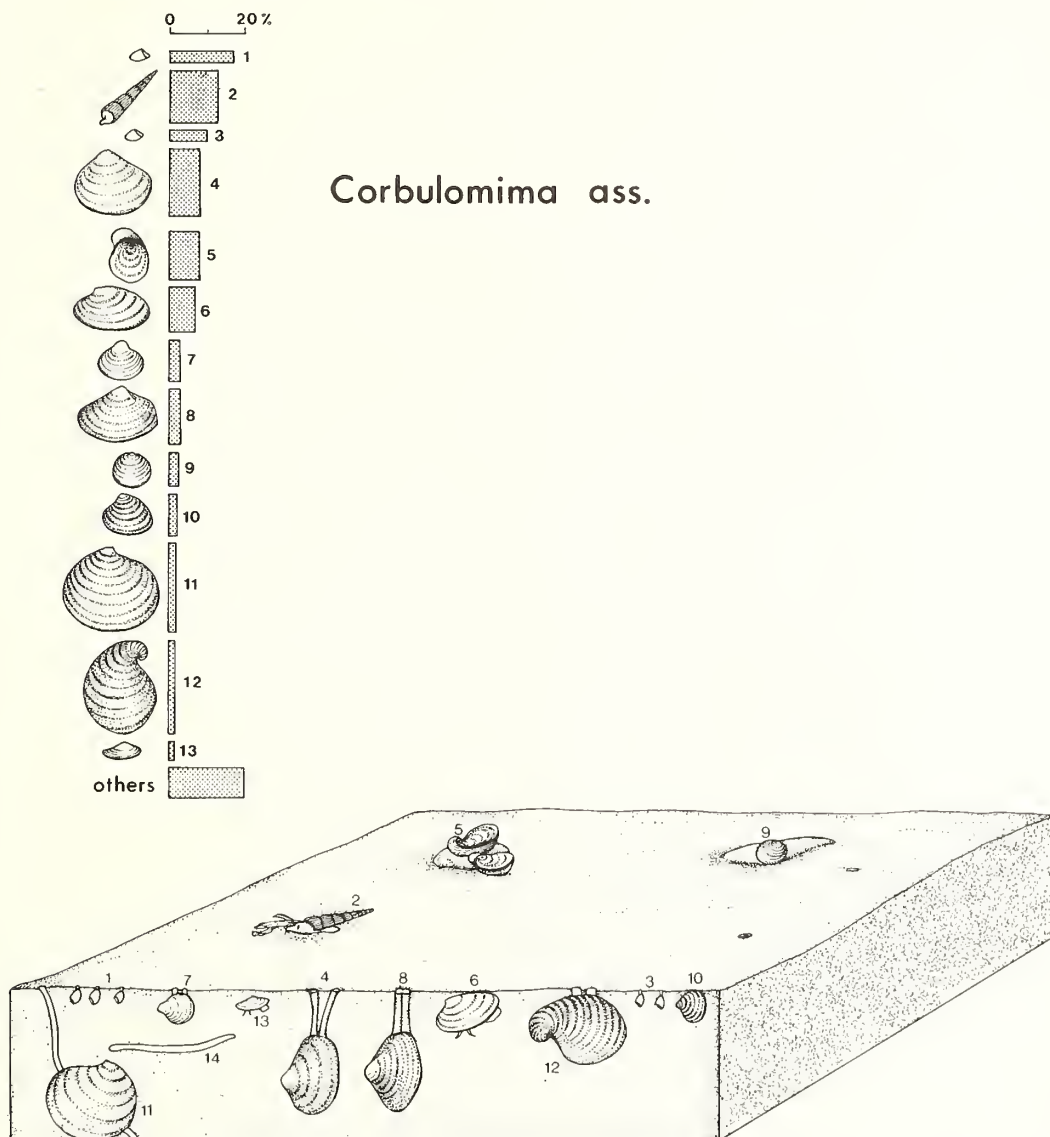
Substrate, algal envelopes, low percentage of bivalved specimens, high fragmentation rate, convex-up orientation, and imbrication of shells testify a high-energy environment for most samples. Lateral transport must have played a role, so that sorting of the fauna certainly took place. Nevertheless a large-scale lateral transport can be excluded, as in some samples *Pseudomelania* are preserved with their calcareous operculum still in place. As many of the oolites are micritic and alternate with thin bands of marly oolite, stable, less rigorous conditions must have prevailed at times which enabled the colonization of the substrate. With return of the high-energy regime, the fauna was then frequently washed out and redeposited under current action. The existence of an ancient *Pseudomelania* community is further supported by a few samples from Dorset where a finer-grained sediment (probably stabilized by the sponge *Rhaxella* whose spicules occur abundantly in the substrate) and a higher percentage of bivalved specimens, together with a low fragmentation rate (20%), indicate a low-energy environment with only little disturbance of the fauna. Thin-shelled burrowing bivalves (*Pholadomya*, *Pleuromya*) are quite common in these samples and indicate that in the collections from the oolites these shells were eliminated during reworking. The reconstruction of the life habits of fossil gastropods is conjectural. The pleurotomariids *Bathrotomaria*, *Obornella*, and *Pleurotomaria* might have been herbivores. Vogel (1968) argued that nerineids belonged to the liberosessile epifauna due to their heavy shell and the manner in which a rudist encrusted the shell of one species. *Nerinella* and other nerineids are usually found in high-energy environments often in association with reefs (e.g. Janicke 1970; see also association Q) which strengthens Vogel's argument. *Ampullina* probably belonged to the epifauna as well feeding on algae or plant detritus, scavenging or even predating. The high-spined, thick-shelled *Pseudomelania* in turn could well have lived as a very shallow burrower feeding by ciliary activity, whilst the species of *Procerithium* present was probably a deposit-feeder. The large number and diversity of gastropods in the *Pseudomelania* association accounts for the large number of trophic groups present: deposit-feeders, suspension-feeders, herbivores (*Bathrotomaria*), and possibly scavengers (*Ampullina*?). Two feeding levels can be distinguished: infaunal deposit-feeders represented by *Nucleolites*, *Teichichnus*, *Cylindrichnus*, *Planolites*, and *Chondrites*, and low-level suspension-feeders (e.g. *Pseudomelania*, *Pleuromya*).

N. *Corbulomima* association

Description. Five collections with 836 specimens constitute the *Corbulomima* association. The very diverse trophic nucleus (text-fig. 23) contains thirteen species starting with *Corbulomima* sp. A, *Procerithium* (*R.*) *struckmanni*, *C. suprajurensis*, *Tancredia subplanata*, *Nanogyra nana*, and *Palaeonucula menkii*. The remaining seven species (*Protocardia dyonisea*, *Thracia depressa*, *Placunopsis duriuscula*, *Trautscholdia extensa*, *Discomiltha rotundata*, *Cercomyopsis striata*, and *Mesosacella* sp.) are of lesser significance (altogether 15.2% of the fauna). Four bivalve species are characteristic of this association, namely *Corbulomima* sp. A, *C. suprajurensis*, *Tancredia subplanata*, and *Palaeonucula menkii*, and one gastropod, *Procerithium struckmanni*. Bivalves (84.7%) and gastropods (14.1%) dominate the association; brachiopods (0.6%), echinoderms (0.4%), and decapods (0.2%) making up the remainder. Trace fossils are present in two of the five collections and consist of *Chondrites* sp., *Planolites* sp., *Teichichnus rectus*, and *Spongiomorpha suevica* var. B. Abundance and diversity of the traces are both medium. The over-all diversity of the benthos is medium (text-fig. 3).

Some pectinids, arcids, free-swimming *Pteroperna*, and *Procerithium* compose the epifauna (31.9%.

text-fig. 21); the association is dominated by the infauna (66.5%), semi-infaunal bivalves (*Pinna*) being fairly insignificant (1.6%). The diverse infauna is represented by shallow-burrowing suspension-feeders (48.8%) like *Corbulomima*, *Tancredia*, and astartids, deposit-feeding bivalves (9.6%; *Mecosacella*, *Palaeonucula*), and less commonly by deep-burrowing suspension-feeders (e.g. *Pleuromya*, *Cercomya*), deposit-feeding gastropods (*Dicroloma*), mucus-tube feeders (*Discomiltha*), echinoids (*Nucleolites*), or brachiopods (e.g. *Lingula*). No specimens occur in life position and only 6.3% are still bivalved. Encrusted and bored



TEXT-FIG. 23. Trophic nucleus and attempted reconstruction of the *Corbulomima* association (N). 1, *Corbulomima* sp. A; 2, *Procerithium struckmanni*; 3, *Corbulomima suprajurensis*; 4, *Tancredia subplanata*; 5, *Nanogyra nana*; 6, *Palaeonucula menkii*; 7, *Protocardia dyonisea*; 8, *Thracia depressa*; 9, *Placunopsis duriuscula*; 10, *Trautscholdia extensa*; 11, *Discomiltha rotundata*; 12, *Ceratomyopsis striata*; 13, *Mecosacella* sp.; 14, *Planolites* sp.

specimens are rare (0.6% and 1.1% respectively); the borers are represented by phoronids and another, unknown organism; the epizoans by *Placunopsis*, *Nanogyra*, and *Serpula*. Fragmentation varies between 50 and 95% and is usually around 80%. Part of the infauna, especially *Corbulomima*, *Pleuromya*, and *Discomiltha*, as well as some gastropods (*Procerithium*) are preserved as steinkerns.

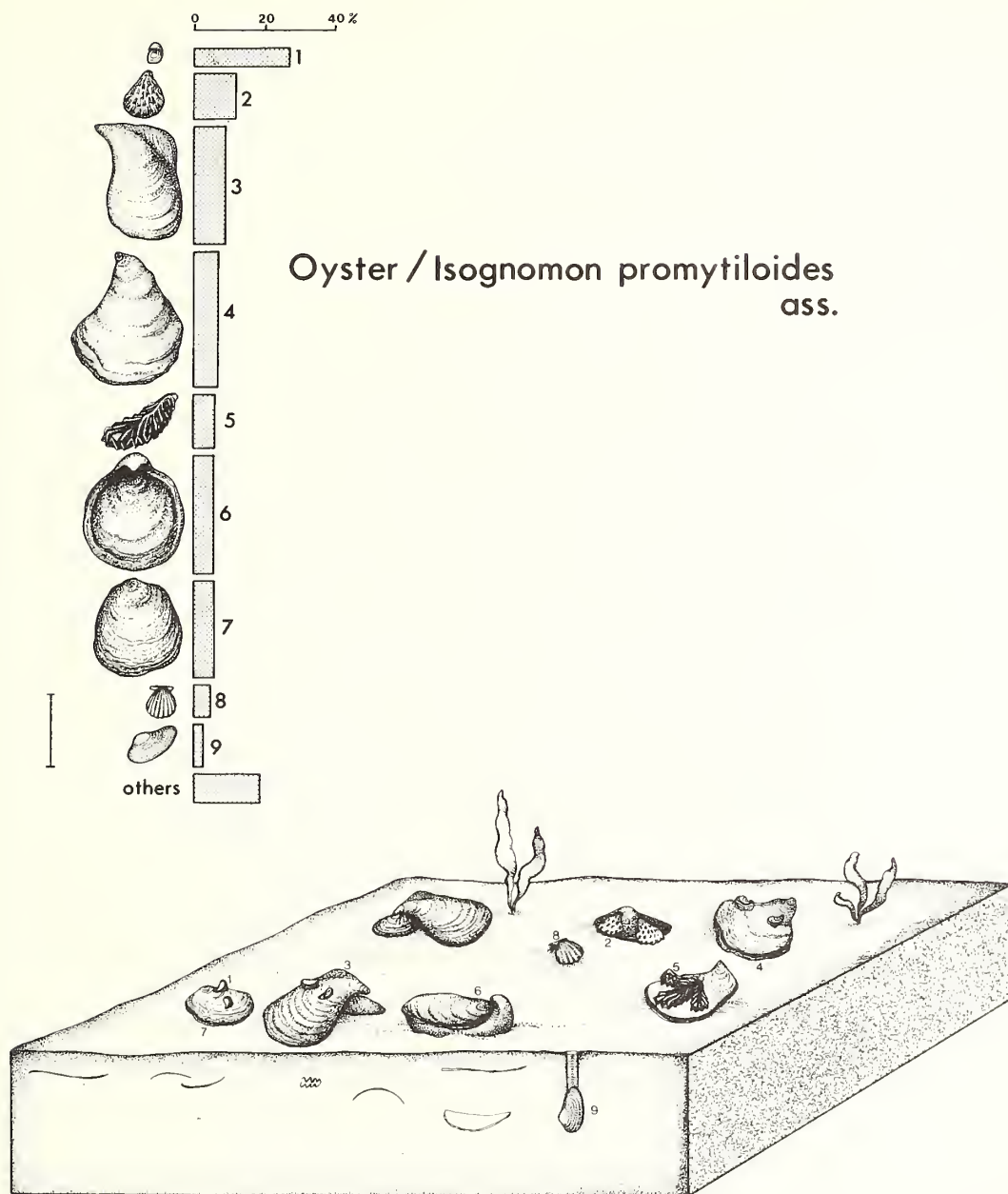
The *Corbulomima* association occurs in a narrow facies range, i.e. in clays, silts, and fine-grained sandstones. One collection, however, was recovered from oolites.

Discussion. The *Corbulomima* association is the only association in the Corallian where infaunal deposit-feeders are significant. This trophic group favours a fine-grained substrate which is also the facies in which they occur in the Corallian. By churning the sediment for food, deposit-feeders increase the water content of the sediment near the depositional interface (Rhoads 1970) and such thixotropic muds are easily suspended even by weak currents. This may be the reason for the low percentage of epifaunal suspension-feeders in this association. Where larger shells provided more extensive substrate for the cemented and byssally attached epifauna, the latter increased in numbers leading to a change in community: these shell pavements are colonized by members of the *N. nana*/*Chlamys* or oyster/*Isognomon promytiloides* associations. The thixotropic muds probably facilitated the winnowing of the mainly thin-shelled infauna even by relatively weak currents. *In situ* reworking or small-scale lateral transport is indicated by the low percentage of bivalved fauna and by the fact that no fauna is preserved in life position. As hardly any shells are bored or encrusted, the rate of sedimentation seems to have been fairly continuous. One collection from the Osmington Oolite Group of Dorset does not fit into the general picture of the environment of the *Corbulomima* association. This collection has been found in high-energy, planar cross-bedded oolites with a very high fragmentation rate (95%). Some shells are worn and quite a few bored (this sample accounts for all bored shells of the association). The shells are found in a lumachelle 2–3 cm in thickness and exhibit size sorting, which indicates that they have undergone transport.

Four feeding levels can be recognized: infaunal deposit-feeders (e.g. *Palaeonucula*, *Mesosacella*), deposit-feeders at the depositional interface (*Discomiltha*, *Procerithium*), low-level suspension-feeders (e.g. *Pleuromya*, *Nanogyra*), and intermediate-level suspension-feeders (*Pinna*).

O. Oyster/*Isognomon promytiloides* association

Description. The oyster/*I. promytiloides* association contains 459 specimens in nine collections. Cemented epifauna dominates the trophic nucleus (text-fig. 24) with *N. nana*, *Plicatula weymouthiana*, and *I. promytiloides* on the first-rank positions. These are followed by *Deltoideum delta*, *Lopha gregarea*, *Gryphaea* (*B.*) *dilatata*, '*Ostrea*' sp., *Chlamys* (*R.*) *fibrosa*, and, finally, *Pleuromya uniformis*. Other cemented bivalves include *L. solitaria*, *Placunopsis radiata*, *P. duriuscula*, '*Ostrea*' *quadrangularis*, and *Praeexogyra* sp. *D. delta*, '*Ostrea*' sp., *P. weymouthiana*, and *I. promytiloides* reach their distribution maxima and are thus characteristic of this association. Except for one brachiopod, the association consists solely of bivalves. Trace-fossil diversity is high, abundance is low. The more important forms include the deposit-feeders *Teichichnus rectus*, *Cylindrichnus concentricus*, *Chondrites*, and the crustacean-made *Spongiomorpha suevica* var. B. The over-all diversity is medium (text-fig. 3). The epifauna (90.4%) dominates the ecological spectrum and is represented by cemented forms (67.1%; see trophic nucleus), byssally attached bivalves (17.0%), and free-living species (e.g. *Gryphaea*; 6.1%). Semi-infaunal bivalves (*Modiolus*, *Gervillia*) are of lesser significance (3.0%) as are deep burrowers (5.0%; e.g. *Pleuromya*, *Pholadomya*). The remaining ecological groups are rare or missing (text-fig. 21). Only 1.3% of the fauna is in life position but 15.03% of the bivalves are preserved with both valves (mainly *Pleuromya*, *Isognomon*, and *Plicatula*). 26.8% of



the fauna are encrusted by a diverse fauna of epizoans such as *L. gregarea*, *L. solitaria*, *Nanogyra*, *Plicatula*, *Placunopsis*, the foraminifera *Nubeculinella*, various serpulids (*Dorso-*, *Cyclo-*, and *Pentaserpula*) as well as the bryozoans *Berenicea* and *Stomatopora*. Phoronids, *Lithophaga inclusa*, and cirripedes bored 9.8% of the fauna. The percentage of fragmentation is high, i.e. between 80 and 98%. Most burrowing species are preserved as steinkerns, the rest with their shell. In some collections part of the epifauna, especially oysters and *Isognomon*, is very worn and intensively bored and encrusted.

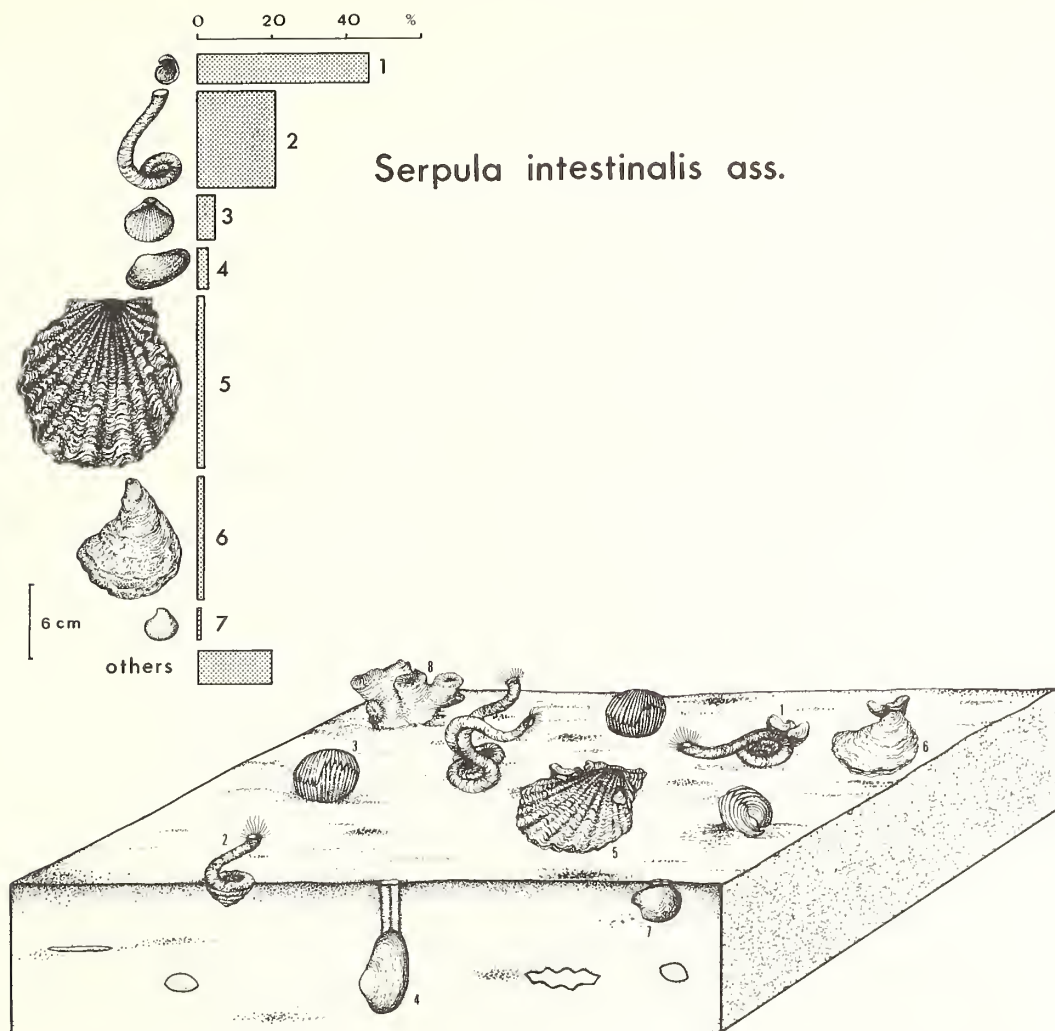
The oyster/*I. promytiloides* association exhibits a clear substrate and facies preference occurring mainly in Fe-oolitic argillaceous limestones and marls.

Discussion. The environment in which most of the oyster/*I. promytiloides* association accumulated was similar to that of the *M. bipartitus*/*P. alduini* and *L. gregarea* associations, i.e. slow sedimentation, a fairly stable, fine-grained substrate, occasional influx of Fe-ooliths, and temporarily high-energy conditions. The slow sedimentation rate led to accumulation of shell material on the sea floor which was often intensively encrusted and bored as well as corroded. Large '*Ostrea*' commonly served as substrate for small clusters of *Lopha*, *Nanogyra*, and *Plicatula*. In some collections, however, excellent preservation of the epifauna, often still bivalved, indicates relatively rapid sedimentation. Transport played only a minor role. The few shell layers present accumulated *in situ* due to non-deposition, rather than through current action. Thus the oyster/*I. promytiloides* association represents again the remnant of an ancient community. An inhomogeneous trophic grouping is the result of the presence of deposit-feeders and suspension-feeders. Two feeding levels could be recognized: infaunal deposit-feeders represented by trace fossils, and low-level suspension-feeders (e.g. burrowing bivalves, *Nanogyra*).

P. Serpula intestinalis association

Description. Four collections with 638 specimens have been grouped into this association which was found only in the uppermost Corallian and lowermost Kimmeridgian of the Dorset coast. The trophic nucleus (text-fig. 25) consists of the ubiquitous *N. nana*, *S. intestinalis*, the brachiopod *Torquirhynchia inconstans*, and the bivalves *Pleuromya uniformis*, *Ctenostreon proboscideum*, *Deltoideum delta*, and *Anisocardia isocardioides*. *S. intestinalis* and *C. proboscideum* only rarely occur elsewhere and *T. inconstans* is confined to this association; these three therefore serve as its characteristic species. Bivalves form 69.6% of the fauna, gastropods 4.5%, brachiopods 4.7%, and free-living serpulids 21.2%. No trace fossils occur except some indistinct tubes most likely left by deposit-feeders. The over-all diversity is medium (text-fig. 3). Semi-infaunal bivalves (1.6%) are represented by *Modiolus*, the infauna (12.4%) by deep-burrowing bivalves (*Goniomya*, *Pleuromya*, *Pholadomya*), shallow-burrowing bivalves (e.g. *Anisocardia*, *Protocardia*, *Isocyprina*), and some gastropods (text-fig. 26). Most species (86.0%) belong to the epifauna. They are either cemented bivalves (48.4%; e.g. the oysters *Nanogyra*, *Deltoideum*), byssally attached bivalves (6.7%; e.g. *Isognomon*, *Chlamys*), free-resting animals like the bivalves *C. proboscideum*, *S. intestinalis*, and some gastropods (e.g. *Bathrotomaria*, *Pleurotomaria*). Another faunal element are small colonies of corals, mainly *Thecosmilia annularis* and *Thamasteria* which occur scattered throughout the samples, especially those from the Ringstead Coral Bed. No specimens of the uncemented fauna occur in life position, but 23.6% are still bivalved. 13.5% of the fauna have been encrusted by the foraminifera *Nubeculinella*, the bivalve *Nanogyra*, and the serpulids *Dorsoserpula*, *Cycloserpula*, and *Pentaserpula*. In addition, specimens of *S. intestinalis* were commonly found to be infested by the hydroid *Protulophila gestroi*. (For detailed discussion of this commensalism see Scrutton 1975). 10.5% of the shells are bored by the bivalve *Lithophaga inclusa*, cirripedes, polychaetes, phoronids, and some unknown organisms. The degree of fragmentation is fairly low and varies between 10 and 50%. Altogether, 15.7% of the fauna are preserved as steinkerns, mainly the infaunal bivalves as well as gastropods and the rare ammonites.

The *S. intestinalis* association exhibits a clear preference for clay with a varying amount of Fe-hydroxide oololiths. In two samples from the basal Kimmeridgian, reworked phosphate pebbles and phosphate steinkerns, partly encrusted with *Nanogyra*, are common.

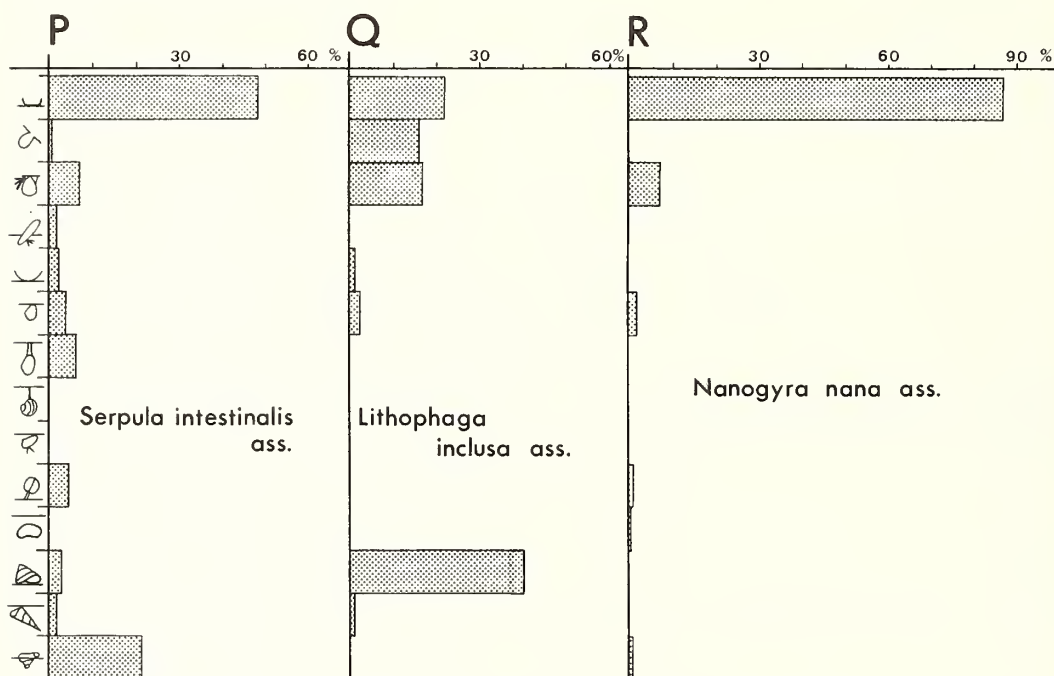


TEXT-FIG. 25. Trophic nucleus and attempted reconstruction of the *Serpula intestinalis* association (P). 1, *Nanogyra nana*; 2, *Serpula intestinalis*; 3, *Torquirhynchia inconstans*; 4, *Pleuromya uniformis*; 5, *Ctenostreon proboscideum*; 6, *Deltoideum delta*; 7, *Anisocardia isocardioides*.

Discussion. The *S. intestinalis* association is tied to a specific environment in which non-deposition and reworking played a certain role. Two collections come from the uppermost Corallian, the Ringstead Coral Bed, the other two from the basal Kimmeridgian, the *Torquirhynchia* Bed. Although Brookfield (1973b) maintains that *Torquirhynchia* occurs only in the basal Kimmeridgian, it has also been found occasionally in the Ringstead Coral Bed. Corals are only found in the latter. They never formed reef-like structures but small isolated colonies growing on a consolidated substrate. In the lower Kimmeridgian, clay was deposited at a very slow rate with occasional influx of Fe-ooliths which are distributed in the form of small seams

in the sediment. Encrusted pebbles and steinkerns indicate that reworking took place. The same association is present in both uppermost Corallian and lowermost Kimmeridgian which indicates that no change in environment took place across the stage boundary (see also Talbot 1973).

S. intestinalis seems adapted to have lived on fine-grained substrate (text-fig. 25). The asymmetry of *Torquirhynchia* is thought to be an adaptation to life in a tidal environment (Brookfield 1973b), but there are doubts as to the validity of Brookfield's interpretation. The relatively high percentage of still bivalved fauna (not only burrowers but also epifaunal species!) suggests that reworking was only on a small scale and that lateral transport was of little significance. Therefore, the *S. intestinalis* association, too, is the autochthonous relic of an ancient community. Only one feeding level can be distinguished: low-level suspension-feeders (*S. intestinalis* burrowing fauna, pectinids). *Bathrotomaria* represent a second trophic group, probably browsing herbivores.

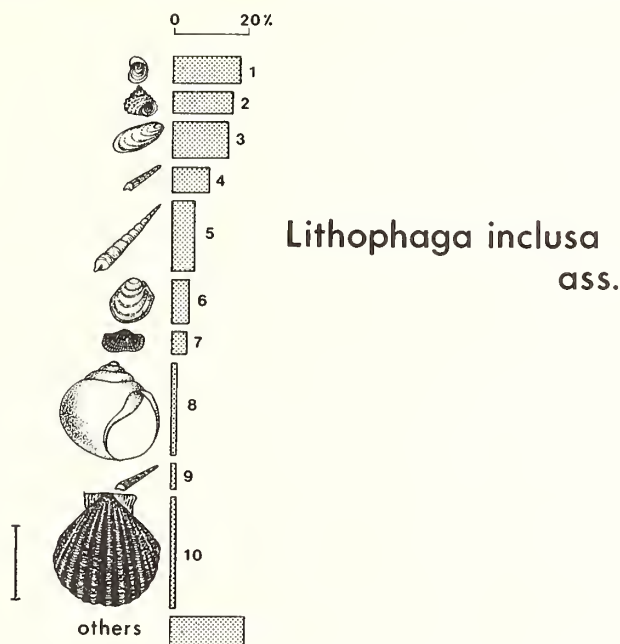


TEXT-FIG. 26. Ecological composition of associations P-R. Legend in text-fig. 6.

Q. *Lithophaga inclusa* association

Description. Represented by 1421 specimens in fifteen collections the *L. inclusa* association has been found in Yorkshire, Oxfordshire, and Normandy. Ten species form the trophic nucleus (text-fig. 27) in which *N. nana* takes the first place followed by *Metriomphalus muricatus*, *L. inclusa*, *Procerithium* sp. 1, *Nerinella* sp., *Plagiostoma zonatum*, and *Barbatia* (Acar) sp. The remaining three species are *Procerithium* sp. 2, *Ampullina* sp., and *Chlamys* (Chl.) *nattheimensis*. *L. inclusa*, *M. muricatus*, and *Procerithium* sp. 1 reach in this association the peak of their distribution and are thus characteristic of it. Bivalves (57.8%) and gastropods (14.9%) dominate the fauna; brachiopods and echinoids are very rare except for abundant

spines of *Plegiocidaris florigemma*. The only trace fossil found, and that only in one collection, is *Chondrites*. The over-all diversity is high (text-fig. 3). The majority (79.4%) of the specimens belong to the epifauna, the rest is infauna as semi-infaunal organisms are very rare (text-fig. 26). The epifauna is shared by cemented bivalves (21.8%; mainly *Nanogyra*), byssally attached bivalves (16.5%; e.g. *Plagiostoma*, *Barbatia*, *Chlamys*), and free-living gastropods (38.5%; e.g. *Metriomphalus*, *Procerithium*). Corals, also members of the epifauna, are very common but have not been included in the statistics. The commonest forms include *Montivaltia* sp., *Thamnasteria concinna*, *Thecosmilia annularis*, *Isastrea explanata*, and *Rhabdophyllia phillipsi*. The infauna (20.4%) is dominated by the rock-boring bivalve *Lithophaga*. Deep- and shallow-burrowing bivalves are of only little significance. 19.8% of the uncemented fauna is in life position, mainly *Lithophaga*,



TEXT-FIG. 27. Trophic nucleus of the *Lithophaga inclusa* association (Q). Length of bar, 4 cm. Because of the complicated nature of reef environments no reconstruction of the association has been attempted. 1, *Nanogyra nana*; 2, *Metriomphalus muricatus*; 3, *Lithophaga inclusa*; 4, *Procerithium* sp. 1; 5, *Nerinea* sp.; 6, *Plagiostoma zonatum*; 7, *Barbatia* sp.; 8, *Ampullina* sp.; 9, *Procerithium* sp. 2; 10, *Chlamys nattheimensis*.

and 29.9% of the organisms are still bivalved (again mainly *Lithophaga*). Only 1% of the fauna excluding corals are encrusted by the foraminifera *Nubeculinella*, the bivalves *Nanogyra* and *Plicatula*, two species of *Serpula* (*Dorsoserpula*, *Cycloserpula*), and the bryozoans *Berenicea* and *Stomatopora*. 0.9% are bored by polychaetes, phoronids, and *Lithophaga*. Fragmentation is usually fairly high, between 75 and 98%. Nearly half the fauna (47.2%) is preserved as steinkerns or moulds, mainly gastropods, arcids, and some burrowing bivalves.

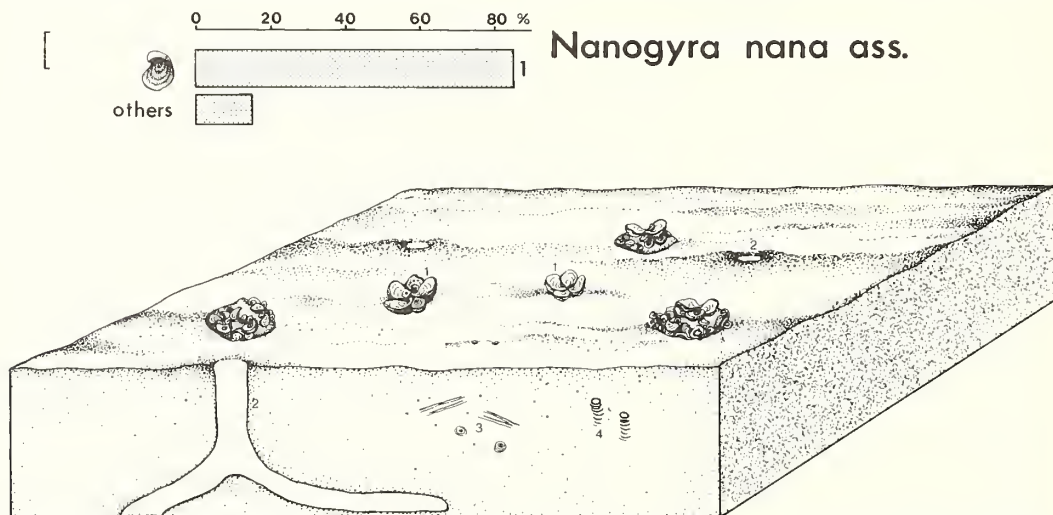
The *L. inclusa* association occurs predominantly in biomicrites and biosparites thus showing a marked substrate preference.

Discussion. As the reef environment in the Corallian will be the subject of a more detailed later study, the discussion here is fairly short. The *L. inclusa* association

has been found in three reefal environments: (a) in the reef itself, (b) in small pockets of lime mud within the reef, and (c) in the reef talus. Autochthonous in the first two environments, it also occurs in form of parautochthonous faunal elements in (c), there usually partly fragmented and worn (e.g. Wheatley Limestone of Oxfordshire and Berkshire). The Corallian reefs, only small structures at the most 6 m thick but usually far less, have been described in detail already by Arkell (1928, 1935) who compared them with Recent reefs in the Red Sea. Arkell also recognized a typical reef fauna which is more or less equivalent to the reef association described here. A reef provides far more niches than the usually fairly uniform sea floor and this is also reflected in the fauna. Herewith a few examples: *Barbatia* (Acar) dwelt as a byssate nestler in crevices amongst corals; *Lithoplaga* and the numerous epizoans found extensive substrate on corals, burrowers like *Protocardia* lived in small pockets of lime mud within the reef and *Metriomphalus muricatus* as well as *Procerithium* sp. 1 were browsers feeding on algae. The description of feeding levels in a reef is a very complex matter but low-level suspension-feeders (burrowing bivalves), and high-level suspension-feeders (e.g. corals) could be distinguished. Herbivores (e.g. *Metriomphalus*) and possibly scavengers (*Ampullina*?) represent two more trophic groups.

R. *Nanogyra nana* association

Description. The *N. nana* association is represented by 3037 specimens in fifteen collections. *N. nana* is the only member of the trophic nucleus (text-fig. 28). Although occurring in nearly all other associations as well, often even as a significant part of the community, it is here that *Nanogyra* reaches the peak of its distribution (85.3%) and is thus the characteristic species. 97.0% of the fauna are bivalves; gastropods (0.5%), brachiopods (0.8%), echinoderms (0.7%), sponges (0.2%), and serpulids (0.7%) forming the rest. Trace fossils are very abundant and diverse, the most important ichnospecies being *Spongiomorpha suevica* var. B, *Cylindrichnus concentricus*, and *Teichichnus rectus*. The over-all diversity is medium (text-



TEXT-FIG. 28. Trophic nucleus and attempted reconstruction of the *Nanogyra nana* association (R). Length of bar, 1 cm. 1, *Nanogyra nana*; 2, *Spongiomorpha suevica*; 3, *Cylindrichnus concentricus*; 4, *Teichichnus rectus*.

fig. 3). Epifaunal cemented bivalves (*Nanogyra* and some other oysters) account for most of the fauna (86.8%) and the only other important group are epifaunal byssally attached bivalves (7.2%; e.g. various species of *Chlamys*). The remaining ecological groups are fairly insignificant, e.g. the infauna totals 3.4% (text-fig. 26). Only 2.9% of the fauna are preserved with both valves, and of the uncemented fauna, only 0.2% are in life position (some deep-burrowing *Pleuromya*). Encrusted are 4.7% of the fauna by one or more of the following epizoans: the oysters *Nanogyra*, *Lopha gregarea*, the serpulids *Cycloserpula*, *Pentaserpula*, *Tetraserpula*, and *Dorsoserpula*, the foraminifera *Nubeculinella*, and thecideacean brachiopods. Only two specimens are bored by the bivalve *Lithophaga inclusa* and cirripedes. Nearly all faunal elements are preserved with their shell except some aragonitic forms (some gastropods and thin-shelled burrowing bivalves). In bioclastic limestones specimens are not infrequently coated with algal envelopes; more rarely specimens are worn.

The *Nanogyra nana* association exhibits a medium substrate range occurring predominantly in sandstones and impure limestones occasionally with shell beds.

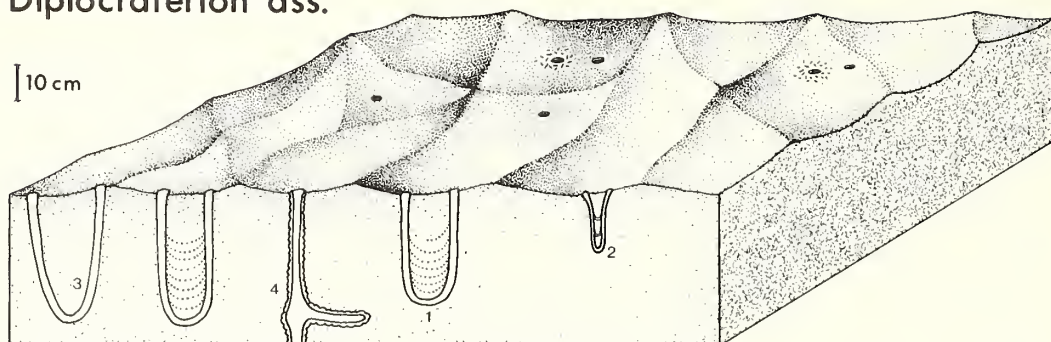
Discussion. The *Lopha gregarea* association (J) has a similar ecological composition to the *N. nana* association (text-figs. 16, 26), but there *L. gregarea* replaces *Nanogyra* as the dominant species. *Nanogyra* must have been adapted to live in a wide range of environments provided that suitable substrate (e.g. shell material) was present. It was probably an opportunistic species, which took over when other species of the same ecological niche (e.g. *Lopha*) could no longer compete, due to unfavourable conditions. An unstable environment is indicated by the low diversity. Which factor was responsible for the eurytopic behaviour is not clear. Settling behaviour of the larvae most likely played an important role. The *N. nana* association probably thrived in a fairly high-energy environment, indicated by the shell beds, specimens with algal envelopes, and coarse sediment. Small-scale transport was probably a frequent event and most collections are the parautochthonous relic of the ancient community. In some cases, however, *Nanogyra* seems to have been embedded more or less in life position, i.e. forming small clusters on an otherwise fairly barren sea floor.

More than 99% of the fauna are suspension-feeders, solely a few *Discomiltha*, *Procerithium*, and trace fossils represent deposit-feeders. Two feeding levels can be recognized: infaunal deposit-feeders (trace fossils) and low-level suspension-feeders (e.g. *Pleuromya*, *Anisocardia*). Some (?) herbivorous gastropods (*Bathrotomaria*) account for a third trophic group.

S. *Diplocraterion* association

Discussion. Fürsich (1975) recognized three trace-fossil associations in the Corallian. Two of them, the *Teichichnus* and the *Rhizocorallium* associations, occur together with associations of the body fauna, the third, however, the *Diplocraterion* association, is not found with any of the associations described under A to R. The *Diplocraterion* association (text-fig. 29) has been found in eleven samples from Oxfordshire, Dorset, and Normandy. It is characterized by burrows of suspension-feeding crustaceans and 'worms', i.e. *D. parallelum*, *D. habichi*, *Spongiomorpha nodosa*, *S. saxonica*, and *Arenicolites variabilis*. Associated with them are *Planolites* sp., and less commonly *S. suevica* var. A and var. B, *Chondrites* sp., and *Cylindrichnus concentricus*. Most of the burrows are deep, and in the case of *D. parallelum* frequently show adjustment to either erosion or sedimentation by vertical shifting of the burrow. Orientation of burrows is encountered occasionally (text-fig. 30). The sediments

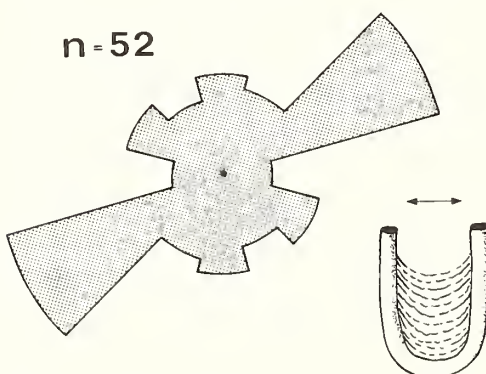
Diplocraterion ass.



TEXT-FIG. 29. Attempted reconstruction of the *Diplocraterion* association (S). 1, *Diplocraterion parallelum*; 2, *Diplocraterion habichi*; 3, *Arenicolites variabilis*; 4, *Spongeliomorpha nodosa* saxonica.

in which the burrows occur are predominantly fine- to medium-grained well-sorted sands and oolites. Sedimentary features are commonly associated with the trace fossils, notably oscillation ripples, large-scale planar or trough cross-bedding as well as herringbone cross-bedding and flaser bedding. The *Diplocraterion* association

occupied a high-energy environment such as very shallow subtidal or intertidal areas (Fürsich 1975). This environment must have been too rigorous for most of the bivalves and gastropods which dominate the remaining Corallian associations. In addition, removal of the body fauna by transport or breakage by frequent reworking could account for the non-preservation of any shells. The harsh environment allowed only animals to flourish which could adjust well to the unstable substrate, i.e. deep and rapid burrowers. Many niches occupied in the other associations are therefore here vacant due to the environmental stress.



TEXT-FIG. 30. Orientation of *Diplocraterion parallelum*. Fallen block from the Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset.

Disturbed assemblages

Only four of the 170 samples collected in the Corallian could not be grouped with any of the above associations. Their usually fairly large trophic nucleus either contains important faunal elements of *several* associations or else indicates selective removal or accumulation of certain elements from *one* association. In both cases, the structure and composition of the original community are distorted. There are two agents which cause disturbed assemblages: (a) currents which cause mixing and/or impoverishment of communities by transportation; (b) reduced sedimentation which causes mixing by superimposition of several communities, that is con-

densation. Both cases are represented, although one or the other assemblage might have been created by a combination of the two agents.

In Table 4 some characteristic features of the four collections are given. When comparing them, sample BH4 from the Osmington Oolite Group at Black Head, Dorset Coast, differs in having the highest fragmentation rate, no bivalved specimens and a different trace fossil suit (suspension-feeders); sedimentary structures are preserved and indicate a high-energy environment. Clearly, this sample is the result of transport especially as the shells form a thin lumachelle in the otherwise unfossiliferous oolite. Sample SPB from the Shell cum Pebble Bed of Beckley, Oxfordshire, in turn, is a typical example of mixing caused mainly by condensation as the low fragmentation rate and the high percentage of still bivalved and encrusted specimens indicate. The remaining two samples occupy an intermediate position and probably both, reduced sedimentation and transport by currents, played a role in their formation. Recognition of disturbed assemblages is of prime importance for environmental interpretation as well as to avoid making mistakes in reconstructing ancient communities and their structure.

TABLE 4. Some characteristics of mixed assemblages.

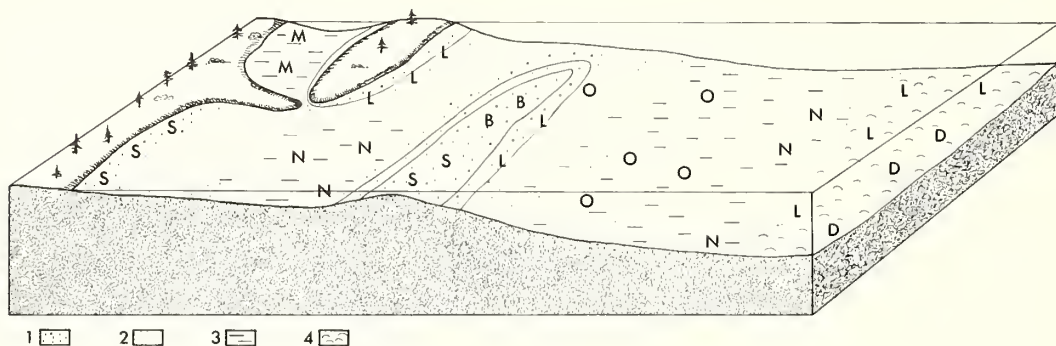
Collection	n _s	Bi-valved %	Life position %	Fragmentation %	Associated sedimentary structures	Trace fossils	Encrusted %	Origin by
BH 4	9	0	0	95	Large-scale planar cross-bedding	<i>Skolithos</i> , <i>Arenicolites</i>	9.90	Transport
BH 31	6	7.47	0	70	None	<i>Chondrites</i> <i>Planolites</i>	9.04	Transport and condensation
BH 25	13	11.64	0	90	None	<i>Chondrites</i> , <i>Planolites</i>	9.84	
SPB	10	20.20	0	50	None	<i>Planolites</i>	27.77	Condensation

n_s = number of species in the trophic nucleus.

ENVIRONMENTAL DISTRIBUTION OF CORALLIAN BENTHIC ASSOCIATIONS

The value of the associations as environmental indicators and their relationship to various facies types has been discussed elsewhere (Fürsich 1976b) so that only a summary is presented here. When the distribution of the associations was plotted against the sections of the Normandy and Dorset Corallian no cyclic sequence (representing transgressive and regressive phases) could be observed, in contrast to the sedimentary and trace-fossil evidence (Talbot 1973; Fürsich 1976b). Thus it seems that within shallow-water deposits of only moderate variations in depth the benthic fauna is not a useful tool for interpreting bathymetry. This is partly due to the fact that some abundant epifaunal species (e.g. *Chlamys*, *Nanogyra*) occur in a wide variety of substrates and that the others, though substrate-related, are not necessarily depth-related.

Despite this, several associations proved to be characteristic of certain environments, especially when certain types of substrates were commonly found in a characteristic bathymetric position. The distribution of these associations in the Corallian is shown in text-fig. 31. For instance, the *Pseudomelania heddingtonensis* association (M) is characteristic of lagoons with lime mud or of sheltered lagoon-like environments. The oyster/*Isognomon promytiloides* association (O) in turn preferred offshore muds and sands. Offshore condensed calcareous sandstones and sandy limestones were populated by members of the *Myophorella clavellata* (D) and *Pleuromya uniformis* (L) associations. The latter is also typical of subtidal sands, whilst the *Corbulomima* association (N) preferred silty muds of low-energy bays or the offshore shelf. High-energy environments such as near intertidal bars or intertidal sands and



TEXT-FIG. 31. Facies distribution of some Corallian associations. B = *Pinna* ass.; D = *Myophorella clavellata* ass.; L = *Pleuromya uniformis* ass.; M = *Pseudomelania heddingtonensis* ass.; N = *Corbulomima* ass.; O = Oyster/*Isognomon promytiloides* ass.; S = *Diplocraterion* ass.; 1, sand; 2, silt; 3, clay, argillaceous/micritic limestones; 4, condensed sandstones and limestones.

silts were usually devoid of body fauna but exhibit a distinct trace-fossil suite, the *Diplocraterion* association (S). The *Pinna* association (B) is typical of a similar environment, i.e. current-swept near intertidal bars. Finally, the *Lithophaga inclusa* association (Q) is restricted to the patch reef environment and to coral thickets or low coral biostromes. In contrast, several associations were found to be fairly independent of the environment. They consist mainly of epibenthic bivalves (e.g. in the *Chlamys/Nanogyra nana* (G) and *N. nana* (R) associations) and occur over most of the Corallian. Thus several Corallian benthic associations, although not useful as bathymetric indicators, are indicative of particular facies and thus aid the reconstruction of the palaeogeographic and environmental set-up of the Middle and Upper Oxfordian of north-west Europe.

COMPARISONS WITH OTHER MESOZOIC BENTHIC ASSOCIATIONS

Benthic community studies have been carried out especially in the Silurian, Cretaceous, and the Recent. Different approaches and presentation of data make a straightforward comparison very difficult as does the degree of splitting or lumping of data

into 'communities'. Furthermore, often only part of the fauna, for instance, brachiopods (e.g. Calef and Hancock 1974; Boucot 1975), has been taken into consideration, and other elements like the infauna have been neglected. Some standardization is needed in the approach to associations, as well as an agreement on the definition of benthic associations or 'communities'. Only then can direct comparison between benthic associations become meaningful and allow sound inferences about community evolution. Thus the following comparisons are of a tentative nature only.

The Lower Oxford Clay associations (Callovian) of central England. As no other Middle and Upper Oxfordian data are available yet, the nearest comparison is with the Lower Oxford Clay associations of central England (Duff 1975). Duff divided the fauna into ten biofacies associations, some of them showing only slight variations in faunal composition. For instance, the difference between the blocky claystone, *Meleagrinnella* shell bed, and the deposit-feeder bituminous shale biofacies consists in the different order in which faunal elements are arranged in the trophic nucleus. As we know from present-day communities, the faunal composition of samples from the same community can vary to a large extent; thus the three biofacies types might represent only variations of one association. None of Duff's associations are found in the Corallian but his *Grammatodon*-rich bituminous shale biofacies resembles to some extent the *Corbulomima* association (N). Both have, in prominent position, an epifaunal (?) deposit-feeding gastropod (*Procerithium*), the small infaunal suspension-feeding bivalve *Corbulomima*, and the infaunal deposit-feeder *Palaeonucula*. Other genera of the trophic nucleus common to both associations are *Mesosacella* and *Thracia*. Pendent bivalves like *Meleagrinnella* and *Bositra* in the Callovian are represented by *Pteroperna pygmaea* in the Corallian but are there of lesser significance. The *Corbulomima* association also resembles, to some extent, the Callovian Nuculacean shell bed and *Grammatodon* shell-bed biofacies which also consist of similar faunal elements. The substrate is identical in the Corallian and Callovian (i.e. mud), and so is the bathymetric position, i.e. low energy but well-aerated offshore subtidal.

Middle and Upper Jurassic bivalve associations of Wyoming and South Dakota. Wright (1973, 1974) distinguished six bivalve assemblages, mainly from the Middle Jurassic of Wyoming and South Dakota which inhabited open shelf, littoral, and lagoon areas. The Bajocian *Pleuromya subcompressa* assemblage is similar to the Corallian *P. uniformis* association, both being relatively diverse and having roughly equal numbers of epifauna and infauna. Genera common to both trophic nuclei are *Pleuromya* and *Gryphaea*. *Camptonectes* in the Bajocian is replaced by *Chlamys* in the Corallian, *Ostrea* by *Deltoideum*. The *P. subdepressa* assemblage inhabited the open-shelf living on firm lime mud, which is also the environment in which part of the *P. uniformis* association in the Corallian is found.

Coloradoan (Cretaceous) macroinvertebrate assemblages from the Central Western Interior. Kauffman (1967) described twenty-six macroinvertebrate assemblages from the Cretaceous of the Central Western Interior of U.S.A. of which at least two have counterparts in the Corallian. His *Pinna* assemblage (K) is dominated by *Pinna* and occurs in shallow-water massive sandstones which is exactly the environment of

the Corallian *Pinna* association (B). His plicate oyster assemblage (M) consisting mainly of *Lopha* which formed local clusters and restricted biostromes on many shallow-water nearshore calcarenites may be compared to the Corallian *Lopha gregarea* association (J) which similarly formed small biostromes but obviously inhabited a somewhat quieter and deeper offshore environment with a mud substrate (Fürsich 1976b).

Lower Cretaceous benthic communities from the Southern Western Interior Basin. Scott (1974) recognized an *Arenicolites* association indicative of the upper shoreface when studying the benthic faunas in the Lower Cretaceous of the Southern Western Interior of the U.S.A. This association can be compared with the Corallian *Diplo-craterion* association which is also devoid of body fauna and indicative of a high-energy environment. The Corallian *Corbulomima* association combines most elements of Scott's (1970, 1974) *Corbula-Breviarca* and *Nucula-Nuculana* associations, consisting mainly of shallow infaunal suspension-feeders and infaunal deposit-feeders. Both of Scott's associations and the *Corbulomima* association occur in the same substrate (mud, clayey silty sandstones) and roughly similar environments (lower shoreface to open sea).

CHARACTERISTIC FEATURES OF THE CORALLIAN ASSOCIATIONS

1. *Nanogyra nana*. In most associations, the oyster *N. nana* occupies one of the first ranks of the trophic nucleus, except for the *Pinna*, *Discomiltha*, and *Corbulomima* associations. Usually, *Nanogyra* forms clusters either on the sediment or on other shells; shells covered with spat are quite frequent. The widespread occurrence and mode of distribution indicate that *Nanogyra* most likely acted as an opportunistic species (Levinton 1970) being extremely eurytopic and having few requirements besides hard substrate and more or less fully marine conditions. A similar distribution pattern and mode of life is recorded of small *Exogyra* (e.g. *E. columbella*) from the Cretaceous of the Central Western Interior (Kauffman 1967). These species might have filled the niche in the Coloradoan, which was occupied by *Nanogyra* in the Corallian.

2. *Chlamys*. Another conspicuous element of the Corallian fauna are several species of *Chlamys*, being the dominant group amongst the byssally attached epifauna. Not only characteristic of the *Chlamys/N. nana* association (G), they also occur in most trophic nuclei of the other associations. Although *Chlamys* ranges from the Triassic to the Recent, it does not play a role in the Cretaceous macroinvertebrate associations so far studied (Kauffman 1967; Scott 1970, 1974) nor in the other Jurassic benthic associations (Wright 1973, 1974; Duff 1975). The absence of *Chlamys* from the Lower Oxford Clay is most likely the result of a lack of suitable substrate (they are also rare in the Corallian *Corbulomima* association which occurs in a similar facies). In the Middle and Upper Jurassic of Wyoming and South Dakota the niche seems to have been filled by *Camptonectes* which are very widespread, and form the dominant element of the *C. bellistriatus* assemblage (Wright 1974).

3. *Scarcity of brachiopods and crinoids*. Brachiopods and crinoids are virtually absent from the Corallian of England and Normandy except for two horizons:

Torquirhynchia inconstans is a common faunal element in the top Corallian and basal Kimmeridgian, and clusters of the rhynchonellid *Thurmanella* dominate, together with *Nanogyra*, part of the Hambleton Oolite of Yorkshire. In the latter horizon the crinoid *Millericrinus* is also a conspicuous faunal element. The appearance of *Torquirhynchia* at the Oxfordian/Kimmeridgian boundary in England and Normandy most likely is connected to the transgression which took place at the base of the Ringstead Coral Bed (Talbot 1973) and which enabled the asymmetric and therefore specialized *Torquirhynchia* to spread over a large area. Species of *Torquirhynchia* have been found, in similar stratigraphical positions, over much of Central and Western Europe, and possibly on the Russian platform (Childs 1969). The abundance of *Thurmanella* in certain beds of the Hambleton Oolite forming small clusters suggests that it, too, can be regarded as an opportunistic species especially as the other main faunal component is *N. nana*. This assumption is also supported by the low diversity of the fauna (see also Fürsich 1976a).

The scarcity of brachiopods and crinoids, both stenohaline groups, seems to point to lowered salinity as the reason for their restricted distribution. However, other stenohaline groups like ammonites, starfish, and especially echinoids, are not uncommon and in the latter case even form distinct associations, so that changes in salinity do not seem to be responsible. Unsuitable (shifting) substrates can also be discounted, as byssally attached bivalves are very widespread. Brachiopods constitute an important part of the fauna of the sponge reefs on the Swabian Alb and also on the high-energy carbonate platform of the Swiss Jura Mountains (author's field observation), both in age comparable to the Corallian. The deeper bathymetric position of the sponge reefs, where brachiopods dominate the epifauna, suggests that there brachiopods still held the niches which were occupied by bivalves in the shallower parts of the epicontinental sea. However, this niche replacement cannot explain the abundance of brachiopods in the very shallow carbonate platform sediments of the Swiss Jura Mountains during parts of the Middle and Upper Oxfordian. In equivalent environments in Dorset and Normandy (e.g. Osmington Oolite Group, Oolithe de Trouville) brachiopods do not occur. Differences in food supply combined with competition with the more efficiently feeding bivalves cannot explain this distribution pattern either, as near landmasses (in the case of England and Normandy) food supply was surely at least equivalent to that on the Swiss carbonate platform which bordered the Tethys. The least unsatisfactory explanation which can be offered is that the articulate brachiopods with their very short free-swimming larval period (probably a few hours or at the most a few days according to Rudwick 1970) were at a great disadvantage when colonizing large areas. When dispersal took place from a source area near the border Tethys/epicontinental sea—and the continual decrease of the abundance of brachiopods from Switzerland through France into England seems to support this—the short free-swimming larval stage, combined with competition from bivalves and unstable environments (due to several transgressions and regressions) might account for the scarcity of brachiopods over most of the Corallian of England and Normandy.

Articulate brachiopods are also rare in the Lower Oxford Clay of Central England (Duff 1975), probably due to the unsuitable substrate which presented difficulties in anchorage for most species and could easily clog their filter-feeding system.

Except for *Kallirhynchia myrina* in the late Callovian and early Oxfordian, brachiopods form no part of the benthic assemblages of the Middle and Upper Jurassic of Wyoming and South Dakota (Wright 1973), perhaps also for similar reasons as in the Corallian. Brachiopods are of no importance in any of the Cretaceous benthic assemblages. Perhaps their role in the Jurassic and Cretaceous epicontinental sea was chiefly confined to their appearance as opportunistic species, or specialists not being able to compete with bivalves under other ('normal') circumstances.

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APPENDIX

Localities of collections

Yorkshire:

- FB Cliffs at Filey Brigg, North of Filey (TA 131 815)
TB I Betton Farm Quarries, Ayton (TA 002 856 and 001 855)
TB II Crossgates Quarry, Seamers (TA 028 843)
P I Disused quarries on Stonygate Moor (SE 868 849)
P II Newbridge Quarry, Pickering (SE 800 860)
NG North Grimston Hill Quarry (SE 84 67)
SQ Spaunton Quarry (SE 722 868)
WQ Whitewall Quarry (SE 791 697)
NRC Nunnington Railway Cutting (SE 649 787)

Oxfordshire/Berkshire:

- SH Shellingford Cross Roads Quarry (SU 326 940)
CH Cothill Quarry (SU 467 997)
B Beckley Quarry (SP 570 108)
CR Cross Roads Quarry, Oxford (SP 550 064)

Dorset:

- BC Cliffs east of Bowleaze Cove (SY 708 818)
- HC Redcliff Point (SY 711 816)
- RB Ringstead Bay (SY 755 813)
- OS Cliff east of Osmington Mills (SY 737 816)
- OSM Cliff at Osmington Mills (SY 735 816)
- BR Cliff at Bran Point (SY 742 813)
- SC Cliff below Sandsfoot Castle, and cliffs towards Weymouth (SY 675 774)
- EF Low cliffs at East Fleet, Weymouth (SY 652 772)
- BH Cliffs between Black Head (SY 729 819) and Shortlake (SY 722 819)

Normandy:

- HLF Cliffs (Falaises des Vaches Noires) between Houlgate and Villers-sur-Mer, 90 m west of the steps leading down to the beach from the camping 'Les Falaises'.
- HLC Cliffs (Falaises des Vaches Noires) between Houlgate and Villers-sur-Mer, 500 m west of the steps leading down to the beach from the camping 'Les Falaises'.
- V Cliffs (Falaises des Vaches Noires) south-west of Villers-sur-Mer.
- BV Low cliffs between Blonville-sur-Mer and Bénéville-sur-Mer.
- MC Small quarries on the slopes of Mount Canisy
- HV Cliffs between Trouville-sur-Mer and Hennequeville

THE CONIFERS *FRENELOPSIS* AND *MANICA* IN THE CRETACEOUS OF PORTUGAL

by K. L. ALVIN

ABSTRACT. *Frenelopsis* Schenk has been used to accommodate various species of fossil conifers with segmented shoots and small scale-like leaves at the nodes. As a contribution to the revision of conifers of this type, some of which probably have an affinity with *Hirmeriella* Hörhammer, the species from the Cretaceous of Portugal are here redescribed. Four species are now recognized: three (one tentatively) are retained in *Frenelopsis*, while the fourth, with spirally instead of cyclically arranged leaves, is placed in *Manica* Watson.

THE genus *Frenelopsis* was erected by Schenk (1869) for some segmented conifer shoots, somewhat resembling those of the modern genus *Callitris*. Schenk identified his specimens which were from the Cretaceous of the Carpathians as belonging to the same species as those earlier described by Ettingshausen (1852) from the Cretaceous of Austria as *Thuites hoheneggeri*. Since then *F. hoheneggeri* has been reported from various parts of the world and some ten other specific names have been erected. Unfortunately, the genus defined only on the basis of the brief descriptions and drawings in these early publications, has been used to accommodate quite a wide range of species. Recent efforts by a number of palaeobotanists to locate Schenk's and Ettingshausen's original material have so far been fruitless.

An important character of the type material which is uncertain is the leaf arrangement. Some parts of the specimens illustrated in Ettingshausen's paper appear to show leaves in cyclic arrangement with three or four at each node. Schenk describes the leaf arrangement as opposite decussate, but the only illustration that shows it (Schenk, pl. 6, fig. 6) has the appearance of an interpretative diagram and not a drawing of a specimen. Another doubtful character in both Ettingshausen's and Schenk's material is the presence or absence of suture lines or grooves running down the internode from the margins of the leaves above such as occur in modern Cupressaceae. Ettingshausen's figures show such lines, at least on the main axes. Of Schenk's figures, while some show somewhat coarse ridges and furrows, in none, except the small specimen shown in plate 6, fig. 5 which may represent a different conifer, do these look like suture lines. Most modern authors have assumed that the absence of suture lines is a generic character. However, Kon'no (1966) has described a species from Malaysia, *F. malaiana*, with opposite decussate leaves and well-defined suture lines; this I would include in *Cupressinocladus*.

Velenovsky (1888) described *F. bohémica* from the Upper Cretaceous (Cenomanian) of Czechoslovakia. He described it as leafless, but Němejc (1926) redescribing the species showed that the leaves were in whorls of three and that the internodes lacked sutures. Hlušík (1972, 1974) has shown that the correct name of this species is *F. alata* (K. Feistmantel) Knobloch.

Of the several other species which have been described, most have lacked suture lines. Leaf number and arrangement has frequently not been referred to, but in

some it has been shown to be only one per node, e.g. *F. parceramosa* Fontaine (1889).

Dr. Joan Watson, in the course of her revision of the English Wealden flora (unpublished thesis, University of Reading, 1964), encountered a conifer with segmented shoots and small spirally arranged leaves, one per node, which she tentatively identified with Fontaine's species. She has proposed that a new generic name *Manica* Watson (1974) should be used for species resembling *Frenelopsis* but with this different leaf arrangement.

Conifers of the *Frenelopsis* type occur mainly in the Cretaceous, though Barale (1973) has reported *F. rubiesensis* Barale, a species with leaves in whorls of three and no suture lines, from beds of Upper Jurassic age in Spain.

The first record from Portugal of a fossil conifer of the *Frenelopsis* type was by Heer (1881) who described some shoots from the Lower Cretaceous (Aptian-Albian) as a new species, *F. occidentalis*. The same name was used by Saporta (1894) for further specimens from Cercal (Barremian), Nazaré (Cenomanian), and Padrão (Cenomanian). He erected another species, *F. leptoclada* Saporta, for specimens from Caixarias (Aptian) and from San Sebastian, Spain (Valanginian). Lima (1900) recorded specimens which he referred to as *F. occidentalis* Heer from Esgueira (Senonian) but Teixeira (1946) referred these specimens to '*F. aff. hoheneggeri*'.

Romariz (1946) in a revision of the Portuguese *Frenelopsis* species recognized three species: *F. hoheneggeri* (Ettingshausen) from the Lower Cretaceous of Almargem and Olhos Amarelos in which specimens believed to be Heer's (1881) holotype of *F. occidentalis* were included, *F. lusitanica* Romariz from Nazaré (now regarded as Cenomanian), and *F. oligostomata* (Romariz) from the Senonian of Esgueira.

All the available material of *Frenelopsis* in the Museum of the Serviços Geológicos de Portugal has been re-examined. This material does not have catalogue numbers.

SYSTEMATIC DESCRIPTION

Order CONIFERALES

Family ?CHEIROLEPIDACEAE

Both *Frenelopsis* and *Manica* are tentatively classified in this family on the basis of Hlušík and Konzalová's (1976) report of pollen of the *Classopollis* type in male cones attributed to *F. alata* and also similar pollen which Dr. Watson and I have found in male cones attributed to a *Manica parceramosa* (Fontaine) from the English Wealden.

Genus FRENELOPSIS Schenk

Frenelopsis alata (K. Feistmantel) Knobloch

Plate 41, figs. 1-5; Plate 42, figs. 1-6; text-fig. 1A

- 1881 *Sclerophyllum alatum* K. Feistmantel, p. 96; pl. 7, fig. 1a-k.
- 1882 ?*Frenelopsis hoheneggeri* (Ettingshausen): Zeiller, p. 231; pl. 11, figs. 1-10.
- 1888 *Frenelopsis bohémica* Velenovsky, p. 590; figs. 1, 2, 10.
- 1894 *Frenelopsis occidentalis* Heer: Saporta, p. 199; pl. 36, figs. 1, 2.
- 1921 *Frenelopsis bohémica* Velenovsky: Bayer, p. 41; text-figs. 5, 6.

- 1926 *Frenelopsis bohémica* Velenovsky: Němec, p. 133; pl. 1, figs. 1–3; pl. 2, figs. 1–5; pl. 3, figs. 1–4.
1946 *Frenelopsis lusitanica* Romariz, p. 144; pl. 3, figs. 2, 3; pl. 4, figs. 1, 2.
1948 *Frenelopsis lusitanica* Romariz: Teixeira, p. 102; pl. 43, fig. 2, 2a.
1974 *Frenelopsis alata* (K. Feistmantel): Hlušík, pl. 1, figs. 3, 4; pl. 3, figs. 1, 2.
1975 ?*Frenelopsis* (from le Brouillard): Broutin and Pons, p. 10, pls. 1–4 (specimens from le Brouillard).

Locality. Nazaré, Estremadura, Portugal.

Horizon. Cenomanian.

Description. Four good specimens of this species exist in the Lisbon collection. The one figured by Romariz (pl. 4, fig. 2) and also by Teixeira was used in the present study of the cuticle. Some of the specimens are partially pyritized and somewhat decomposed, others are compressed and carbonized. These latter usually show more or less prominent longitudinal furrowing, probably produced by shrinkage at some stage, but the pyritized specimens have a smooth surface.

All the specimens show up to three orders of branching. The stoutest axes are up to 5 mm broad and have segments two to three times longer than broad; they are more or less straight and branched at nearly every node. Lateral branches have longer, narrower segments; these penultimate branches are up to 2 mm wide and somewhat zigzag due to an almost pseudodichotomous mode of branching. The ultimate branchlets, arising singly at almost every node on the penultimate, are about 1 mm wide, with segments many times longer than wide. Branches arise from parent shoots at about 30°, disregarding the zigzag.

There is no doubt that at least the ultimate branchlets had leaves in whorls of three. Plate 41, fig. 1a, b shows two sides of the same node of an ultimate branch. The leaves are triangular, about 0.6 mm wide, 0.3 mm long, and have a fringe of unicellular hairs along the margins (Pl. 41, fig. 4). The leaves are joined laterally to form a sheath as much as 1 mm deep. The form of the leaf-sheath on axes of lower orders is not clear, but its general appearance is similar.

The internode cuticle is about 30 μm in total thickness (measured in folds under the light microscope) with the outer periclinal epidermal wall about 8 μm . Sometimes the cuticle on one side of the specimen appears paler and thinner than that on the other; differences are also seen in the SEM view of the outer surface (cf. Pl. 42, figs. 1, 2). The darker more robust cuticle (represented in fig. 1) looks smooth at low magnification, but at high magnification shows some patterning (just discernible in the figure) suggestive of surface wax, whereas the cuticle from the opposite side (fig. 2) shows furrows marking the outlines of epidermal cells and is without evidence of wax. Whether these differences reflect a degree of dorsiventrality cannot be decided on present evidence. It is probably that side of the shoot which is uppermost and exposed on the block which has the thinner, paler type, and it is therefore possible that the exposed cuticle has suffered some kind of degradation since the specimens were collected. The very limited amount of material at my disposal has precluded any further investigation of this problem.

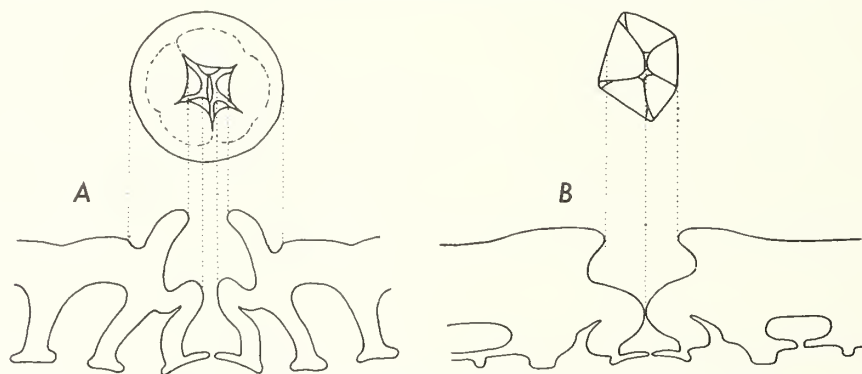
The epidermal cells are very clearly seen in both the light microscope and the SEM. They are rather uniform, mostly slightly elongated, but never more than twice as long as broad; longitudinal rows are fairly well marked, (20–) 25 (–45) μm wide. The anticlinal walls are about 4 μm thick. Though portions of the inner periclinal

walls of the epidermis may be cutinized (Pl. 42, figs. 3, 4), the hypodermis is generally not marked except in the region of the leaf and sheath (Pl. 42, fig. 6).

The stomata are optically denser than the rest of the cuticle and therefore conspicuous in the light microscope (Pl. 41, fig. 2). They are arranged in rather irregular longitudinal rows, the rows being spaced irregularly, with one to four epidermal cells between, and the stomata irregularly spaced (75–150 μm apart) in the rows (Pl. 41, figs. 2, 5).

Stomata continue up on to the base of the sheath but fade out on the teeth-like leaves themselves which were therefore presumably non-photosynthetic. Stomata continue abundantly towards the node below on that part covered by the lower sheath, only ceasing very close to the node.

The stomata are highly specialized, with four to five (or six) subsidiary cells surrounded by a ring of a usually greater number of somewhat specialized epidermal cells. The form of the stomatal pit is shown reconstructed in text-fig. 1A. This is



TEXT-FIG. 1. A, *Frenelopsis alata* (K. Feistmantel) Knobloch. Reconstruction of outside view of stoma and section of cuticle, $\times 500$. B, *?Frenelopsis occidentalis* Heer. Reconstruction of outside view of stoma and section of cuticle, $\times 500$ approx.

based on sections viewed in the SEM (Pl. 42, fig. 5) and also on surface views (Pl. 42, figs. 1, 2) and light microscope observations (Pl. 42, figs. 2, 3). The stomatal pit has a polygonal or more or less stellate mouth surrounded by a lobed canopy. The lobes are not always very distinct, but their number equals that of the subsidiary cells rather than that of the surrounding epidermal cells. I conclude, therefore, that they represent parts of the subsidiary cells. In the throat of the pit is a series of papillae again equal in number to the subsidiary cells. The guard-cell cuticles are thin and

EXPLANATION OF PLATE 41

Frenelopsis alata (K. Feistmantel) Knobloch, from Nazaré (Cenomanian).

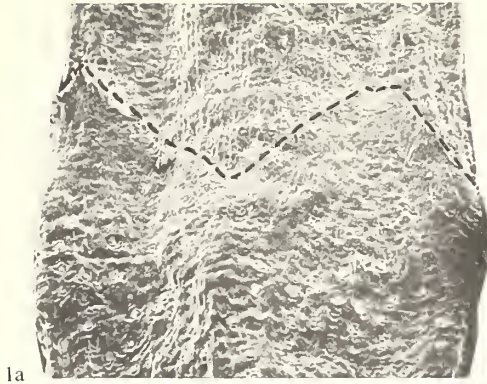
Fig. 1a, b. Two sides of the same node of an ultimate branch. Edges of leaves outlined by broken lines, SEM, $\times 40$.

Fig. 2. Cuticle of internode, light microscope, $\times 200$.

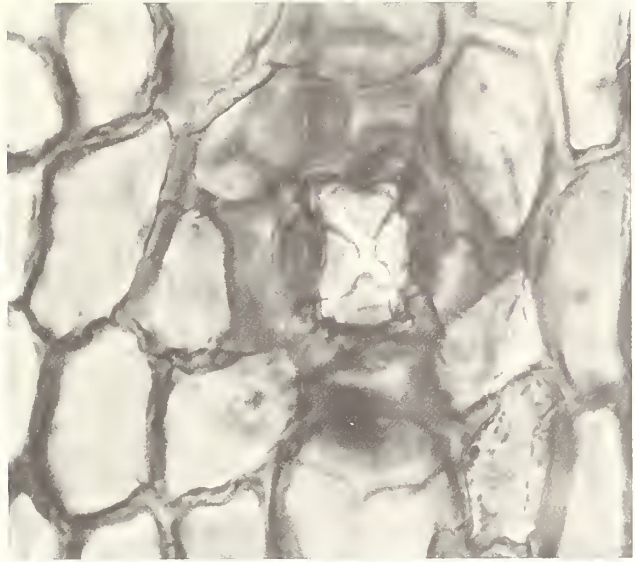
Fig. 3. Stoma, focused through the papillae in the throat of the stomatal pit, light microscope, $\times 800$.

Fig. 4. Edge of leaf, showing short hairs extending from the marginal cells, SEM, $\times 400$.

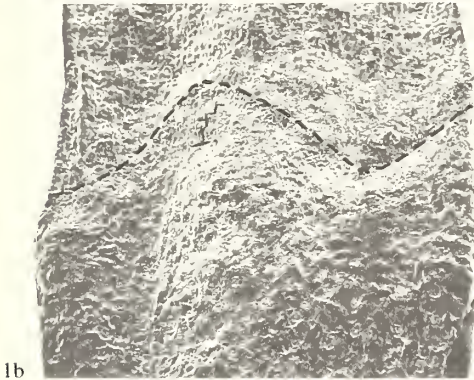
Fig. 5. Inside of internode cuticle, SEM, $\times 200$.



1a



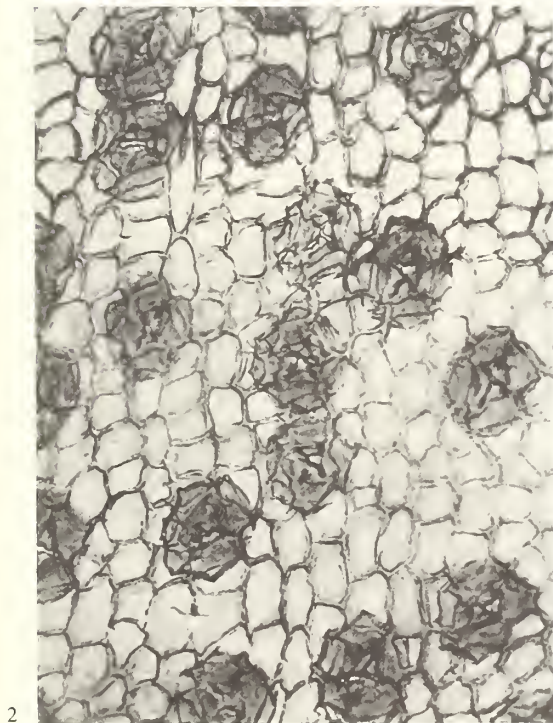
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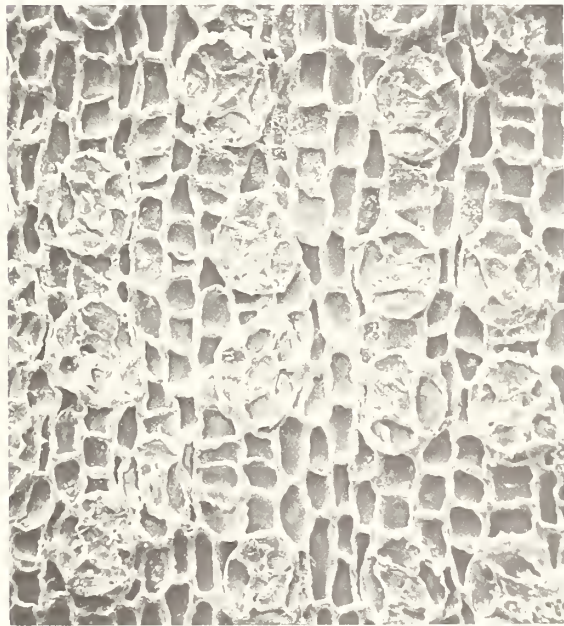
1b



4



2



5

frequently absent in preparations, so that the inside view shows the papillae (Pl. 42, fig. 4). As seen in outer surface view (Pl. 42, fig. 1), the canopy is delimited peripherally by a circular groove, and it is the outer side of the groove which is delimited by the ring of surrounding epidermal cells. This interpretation of the stoma is supported by the appearance of specimens such as that shown in Plate 42, fig. 2 where the anticlinal walls of the epidermis are marked by furrows; clearly here the stoma has five subsidiary cells and six surrounding epidermal cells.

No satisfactory preparations were produced of the adaxial leaf and sheath cuticle, which is delicate, but the adaxial surface appears somewhat papillate and without stomata.

Discussion and comparison. This Cenomanian species is well distinguished from the other Portuguese species. I identify it with the species described from Czechoslovakia now known as *Frenelopsis alata* (for references, see synonymy). Dr. Hlušík has kindly examined photographs of the Portuguese material and agrees that there is a very close resemblance to that recently studied by him (pers. comm.), and with which he has found male cones containing *Classopollis* in association (Hlušík and Konzalová 1976).

It seems to me from the available descriptions (Zeiller 1882; Carpentier 1937) that the specimens described from Bagnols (Turonian) in the south of France may also belong to the same species. These were described by Zeiller as *F. hoheneggeri* (Ettingshausen) and the cuticle was examined further by Carpentier when he described other specimens, again under the name *F. hoheneggeri*, from the Campanian of Sainte-Baume, France. These younger specimens, however, I do not believe are the same, but may be much closer to *F. oligostomata* from Portugal.

The material described by Broutin and Pons (1975) from the Cenomanian of Le Brouillard, France, may also represent *F. alata*, but the form of the stoma is not quite clear from the description so far published.

Frenelopsis oligostomata Romariz

Plate 43, figs. 1-6; text-fig. 2A-D

- 1900 *Frenelopsis occidentalis* Heer: Lima, p. 11 (record only).
- 1937 ?*Frenelopsis hoheneggeri* (Ettingshausen): Carpentier, p. 5; pl. 1, figs. 1-5; pl. 2, figs. 1-3.
- 1946 *Frenelopsis oligostomata* Romariz, p. 144; pl. 5, figs. 1, 2.
- 1946 *Frenelopsis* aff. *hoheneggeri* (Ettingshausen): Teixeira, p. 236; pl. 1, figs. 1-4; pl. 2, figs. 1, 2; pl. 3, figs. 1, 2.
- 1975 *Frenelopsis* (from Esgueira), Broutin and Pons, p. 10, pls. 1-4 (specimens from Esgueira).

EXPLANATION OF PLATE 42

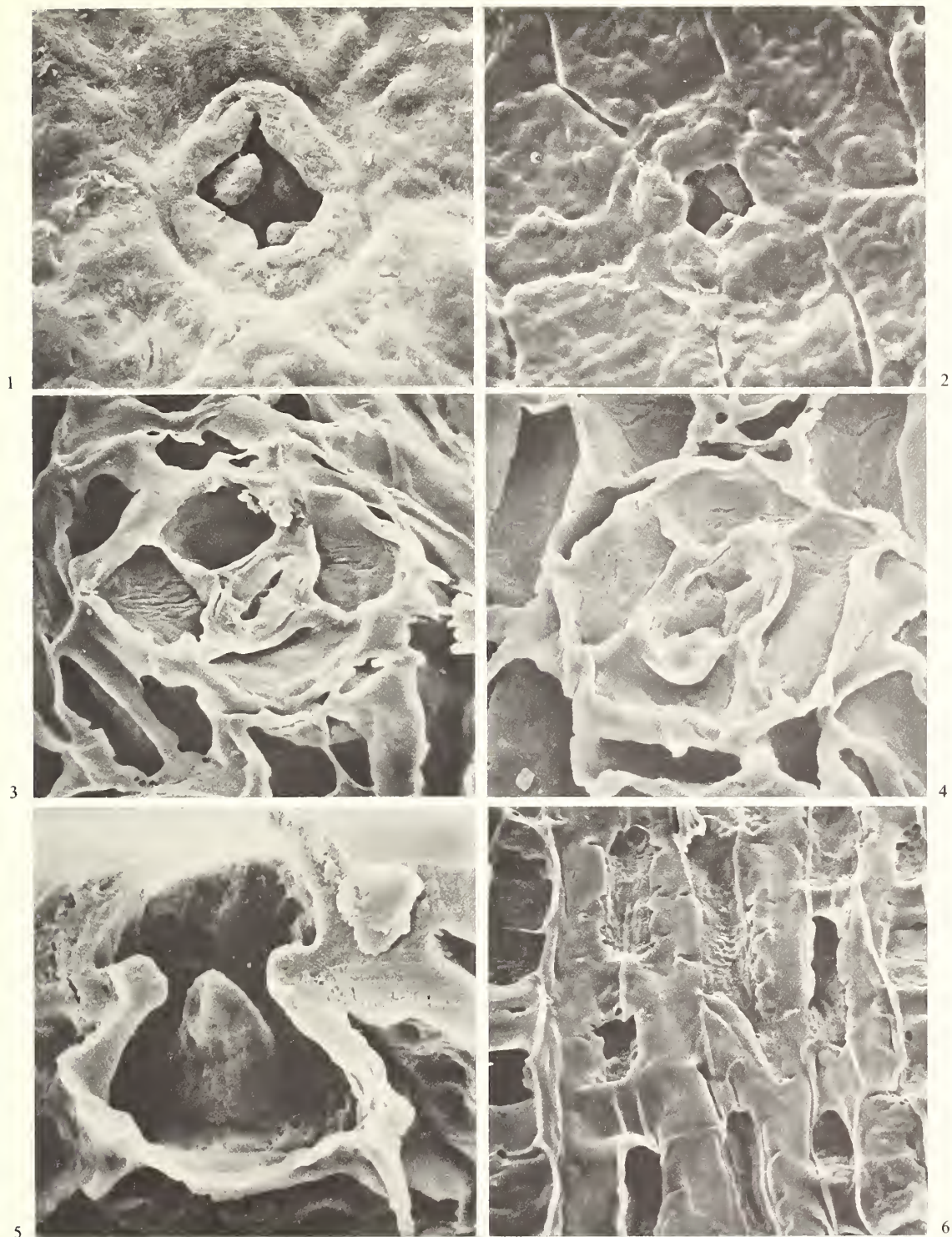
Frenelopsis alata (K. Feistmantel) Knobloch, from Nazaré (Cenomanian).

Figs. 1, 2. Stomata from opposite sides of the same branch segment, SEM, $\times 950$.

Figs. 3, 4. Stomata seen from inside cuticle. Guard cells are absent in fig. 4 and the papillae in the throat of the stomatal pit can be seen, SEM, $\times 900$.

Fig. 5. Vertical section through stomatal pit showing, at top, part of the 'canopy' and mid-way down, three of the throat papillae, two in section and one at the back, SEM, $\times 1600$.

Fig. 6. Abaxial cuticle of leaf showing cutinized hypodermis, SEM, $\times 900$.



ALVIN, *Frenelopsis*

Locality. Esgueira, near Aveiro, Beira Littorale, Portugal.

Horizon. Senonian.

Emended diagnosis. Branching (?penultimate) shoots up to 5 mm wide, somewhat zigzag. Lateral branches (?ultimate) up to 4 mm wide, arising one at each node of the parent shoot at about 30° (disregarding zigzag). Leaves in whorls of three.

Cuticle of internode about 30 μm in total thickness (measured in folds under the light microscope) with the outer periclinal wall of the epidermis about 10 μm . Epidermal cells clearly marked (Pl. 43, figs. 3, 5), mostly isodiametric but rather variable in shape and size (20–45 μm), seldom longer than wide, more frequently wider than long; longitudinal rows not well defined, except for short chains of cells. Anticlinal walls about 8 μm thick. Hypodermis of isodiametric cells sometimes present.

Stomata about the same optical density as the rest of the cuticle (Pl. 43, fig. 5); arranged in longitudinal rows, but rows somewhat obscure due to rather distant spacing of stomata (75–250 μm apart) within the rows (Pl. 43, figs. 3, 5). Subsidiary cells (four) five (or six). Mouth of stomatal pit bounded by a thick, obscurely lobed, wrinkled ring (Pl. 43, fig. 1), the number of lobes equalling the number of subsidiary cells. Papillae in the throat of the pit short, wide, and frequently obscured by a deposit of an opaque, granular substance. Subsidiary cells inconspicuous in the light microscope, but seen clearly from the inside by SEM as wide, convex cells showing faint radial striations (Pl. 43, fig. 4), the convexity corresponding to a thickening of the cuticle of the surrounding epidermal cells just beyond the outermost limit of the raised external ring; the furrow between the ring and the thickened area showing as a light translucent ring in the light microscope (Pl. 43, fig. 6). Guard cells thinly cutinized, only the parts adjacent to the subsidiary cells generally surviving maceration (Pl. 43, fig. 4). Stomatal orientation most frequently transverse.

Stomata present on the lower part of the internode covered by the leaf-sheath of the node below but, at the top of the internode, ceasing rapidly on the sheath; upper part of sheath and leaves therefore probably non-photosynthetic. Sheath and leaf margins fringed with small unicellular hairs extending from the marginal cells (Pl. 43, fig. 2).

Further description and discussion. Of the three specimens all from the same locality, one is well preserved with a cuticle, the others being only impressions. The good

EXPLANATION OF PLATE 43

Frenelopsis oligostomata Romariz, from Esgueira (Senonian).

Fig. 1. Stoma from outside, SEM, $\times 1600$.

Fig. 2. Edge of leaf sheath (below) overlapping internode (above), SEM, 450.

Fig. 3. Inside of internode cuticle, SEM, $\times 180$.

Fig. 4. Stoma seen from inside cuticle, SEM, $\times 800$.

Fig. 5. Internode cuticle, light microscope, $\times 200$.

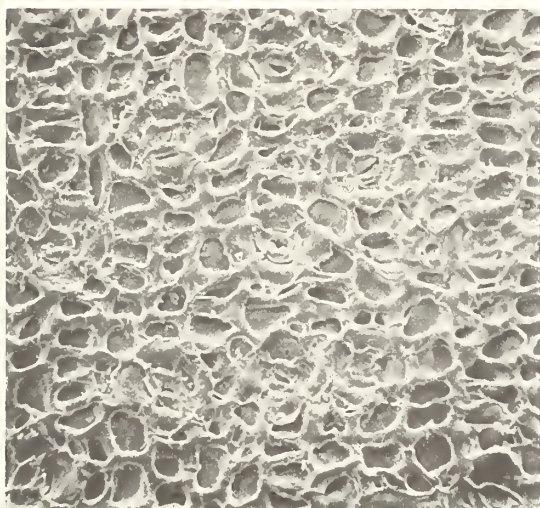
Fig. 6. Stoma, focused through the stomatal pit, light microscope, $\times 800$.



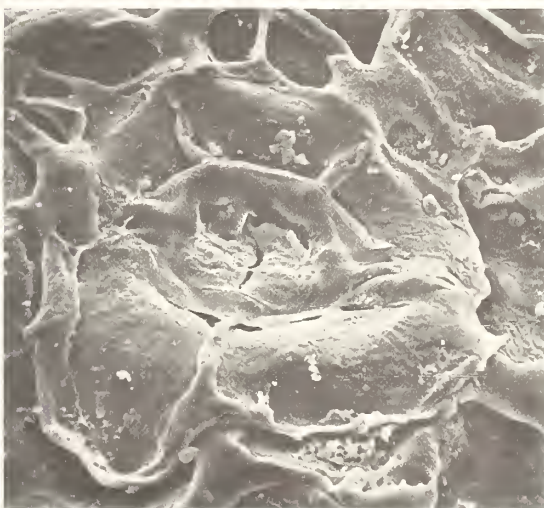
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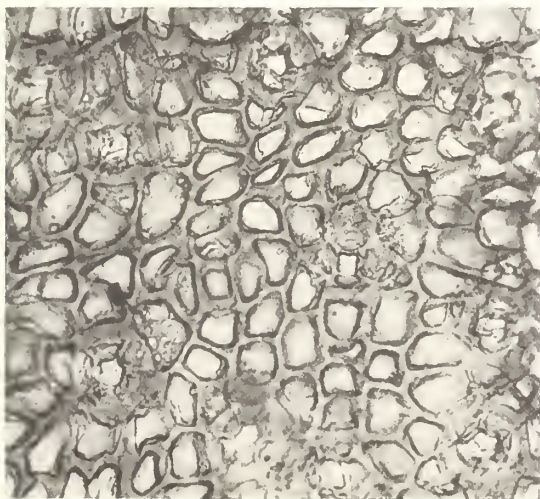
2



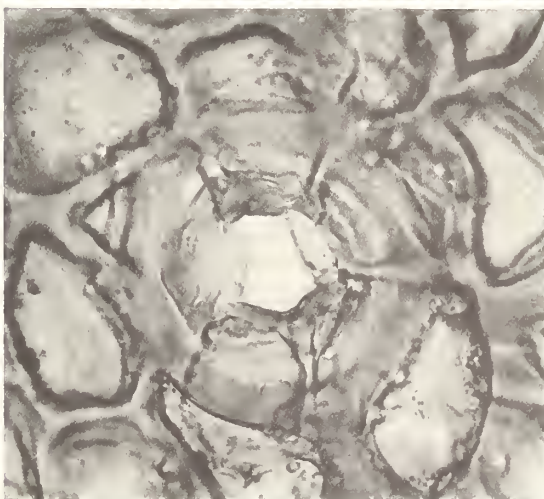
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4

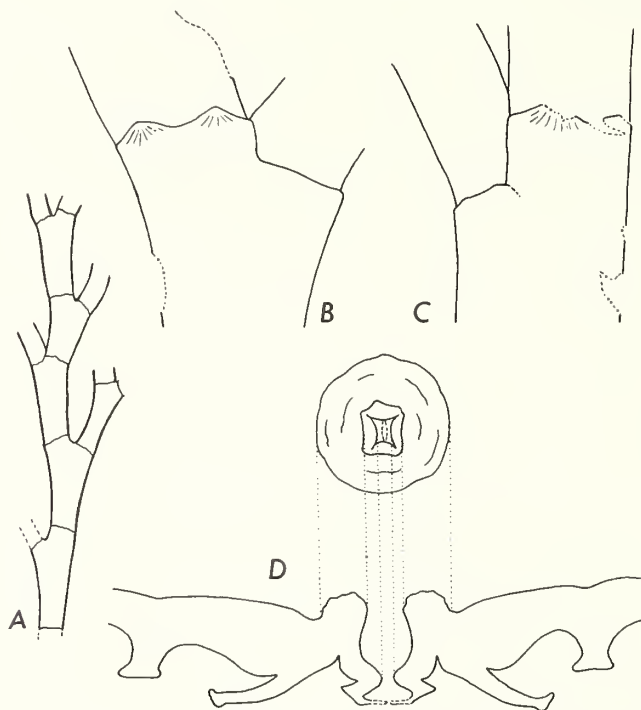


5



6

specimen, used here for cuticle characters and figured in text-fig. 2A-C, was figured by Teixeira (1946) as his plate 1, fig. 1, but not by Romariz, though he probably used this specimen for his cuticle studies. Brontin and Pons (1975) have recently described some new specimens from Esgueira which they have not yet specifically identified. However, it is clear from their description that they represent this species.



TEXT-FIG. 2. *Frenelopsis oligostomata* Romariz. A, outline drawing of specimen. [Part of that figured by Teixeira (1946, pl. 1, fig. 1).] B, C, two successive nodes from the same specimen, $\times 25$. D, reconstruction of outside view of stoma and section of cuticle, $\times 500$.

It was not possible to be quite certain about the number of leaves at the node on the basis of the specimens in Lisbon, but the specimens of Broutin and Pons (1975) make it quite clear that there are three. Text-fig. 2B, C represents two successive nodes. Two short, triangular, striated extensions to the sheath are seen on one side of the specimen at one node (text-fig. 2B), but only one at the next (text-fig. 2C). The relationship of the branch emission to the leaves and sheath is not clear. As text-fig. 2B, C shows, the branch joins the stem at about 1 mm below the level of the top of the sheath. If the branch is axillary, then the sheath must either be attached to the main stem at the level of the branch base and then split by the growing branch, or else it may be attached rather higher but along a line which dips strongly at the subtending leaf.

The stomata, though different in a number of details from those of *F. alata*, are basically comparable (cf. text-figs. 1A and 2D). Their comparative obscurity in the light microscope (Pl. 43, fig. 5) contrasts markedly with their prominence in *F. alata* (Pl. 41, fig. 2). The granular deposit in the stomatal pit was noted by Romariz; it may represent preserved wax.

No satisfactory preparations have been made of the adaxial leaf and sheath cuticles.

No specimens of *Frenelopsis* described from elsewhere can be said to be identical to this species, with the possible exception of those reported from the Campanian of Sainte-Baume, France, by Carpentier (1937). Unfortunately, however, Carpentier's specimens are not very fully described. The epidermal cells are similar in size, shape, and arrangement and in the thickness of the anticlinal walls, but the stomata, the pits of which are blackened by a dark deposit, show few details.

The specimens tentatively named '*F. aff. alata*' by Hlušík (1974) from the Senonian of Czechoslovakia are much more like *F. alata* than *F. oligostomata*.

Genus MANICA Watson

Manica parceramosa (Fontaine) Watson

Plate 44, figs. 1-8; text-fig. 3

- 1889 *Frenelopsis parceramosa* Fontaine, p. 218; pl. 111, figs. 1-5; pl. 112, figs. 1-5; pl. 168, fig. 1.
 1946 (*pro parte*) *Frenelopsis hoheneggeri* (Ettingshausen): Romariz, p. 143; pl. 2, figs. 1, 2; pl. 3, fig. 1.
 1948 *Frenelopsis hoheneggeri* (Ettingshausen): Teixeira, p. 65; pl. 24, figs. 1-3.
 1965 (*pro parte*) *Frenelopsis hoheneggeri* (Ettingshausen): Reymanówna, p. 19; pl. 1, figs. 1, 3, 6; text-fig. 2A, C, E-M.
 1974 *Manica parceramosa* (Fontaine) Watson, p. 428. (Name only.)

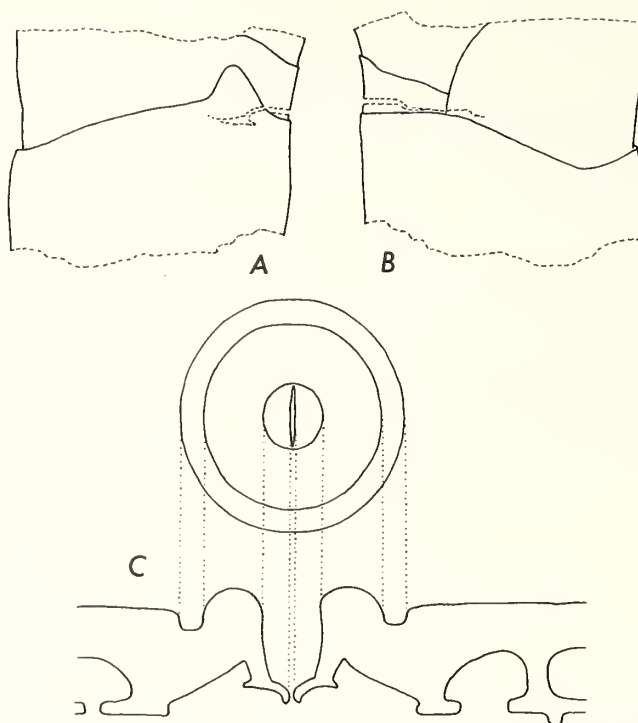
Locality. Olhos Amarelos, near Cabo da Serra, Obidos, Estremadura, Portugal.

Horizon. Aptian-Albian.

Description. Two good blocks exist in the Lisbon collection; one of them was figured by Teixeira (1946) and it is this which I have used in my study. Both blocks bear several short lengths of broken shoots and numerous isolated segments. The shoot segments are 8-10 mm wide and up to about twice as long as wide. At the node is a single, triangular leaf represented by an extension of about 0.8 mm high from the normally continuous, collar-like sheath (text-fig. 3A). Opposite the leaf (text-fig. 3B) the sheath dips to its lowest point, forming a usually shallow sulcus. Occasionally, however, as in the segment above in this same specimen, the sulcus dips right down to the node below so that the sheath is 'open' rather than 'closed'. The leaves are spirally arranged. Branching has not been clearly observed.

The flanks of the leaf and the sheath bear abundant unicellular hairs extending from the marginal cells (Pl. 44, fig. 2).

The internode cuticle is about 30 μm in total thickness (measured in folds under the light microscope) with the outer periclinal wall of the epidermis about 13 μm thick.



TEXT-FIG. 3. *Manica parceramosa* Fontaine. A, B, opposite sides of the same shoot fragment showing parts of two internodes, $\times 6$. C, reconstruction of outside view of stoma and section of cuticle, $\times 500$ approx.

The epidermal cells are clearly seen in the light microscope (Pl. 44, figs. 7, 8) but owing to often strong cutinization of the inner periclinal wall and part of the hypodermis, they are not always clear in the SEM view of the inner surface (Pl. 44, fig. 6). The epidermal cells are more or less isodiametric, but usually elongated (up to twice as long as wide) between the stomatal rows; they are $10\text{--}20\text{ }\mu\text{m}$ wide. The anticlinal walls are about $6\text{ }\mu\text{m}$ thick. Hypodermal cells are most strongly cutinized between the stomatal rows; they are elongated, about $10\text{ }\mu\text{m}$ wide, and marked by thin flanges underlying the epidermal cuticle (Pl. 44, fig. 6).

EXPLANATION OF PLATE 44

Manica parceramosa (Fontaine) Watson, from Olhos Amarelos (Aptian-Albian).

Fig. 1. Internode cuticle from outside showing four stomata, SEM, $\times 420$.

Fig. 2. Edge of leaf-sheath, showing rather long hairs extending from the marginal cells, SEM, $\times 800$.

Fig. 3. Outer surface of adaxial leaf cuticle, SEM, $\times 400$.

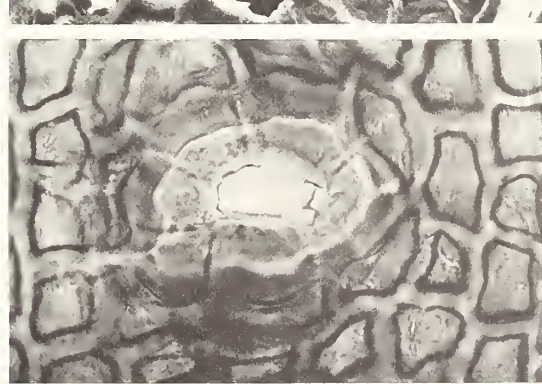
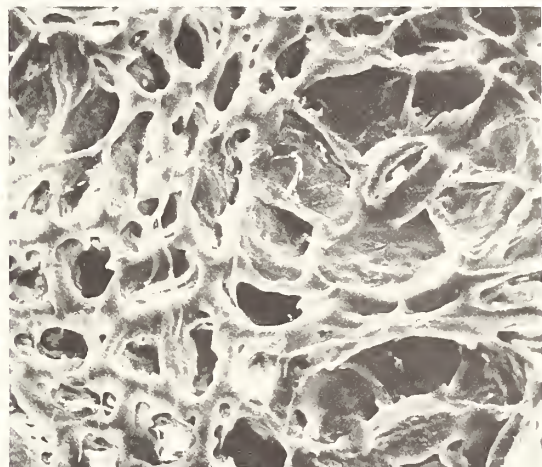
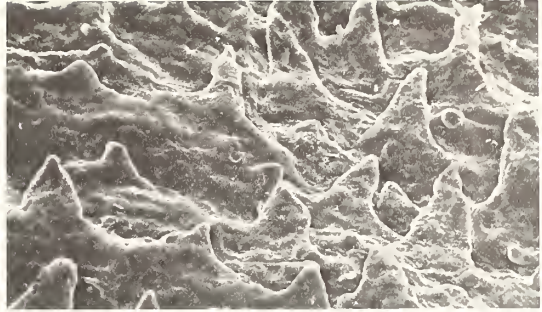
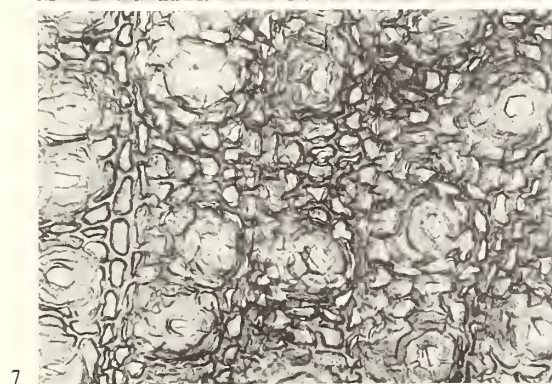
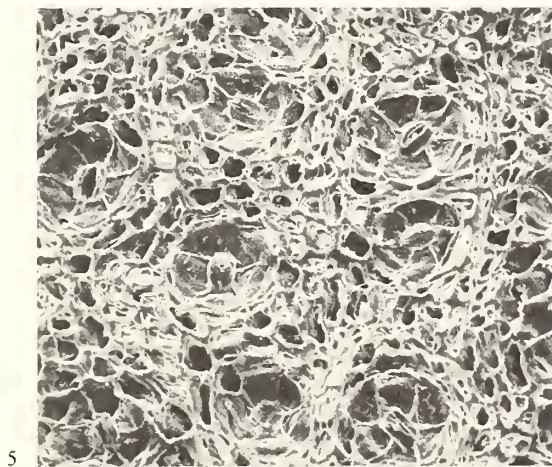
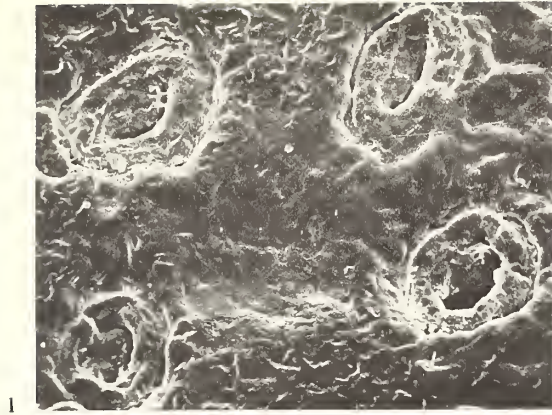
Fig. 4. Inner surface of adaxial leaf cuticle, SEM, $\times 400$.

Fig. 5. Internode cuticle from inside, SEM, $\times 220$.

Fig. 6. Internode cuticle from inside showing two stomata and cutinized hypodermis. Stomata showing ring of subsidiary cells and guard cells, SEM, $\times 550$.

Fig. 7. Internode cuticle, light microscope, $\times 150$.

Fig. 8. Stoma, focused through stomatal pit, light microscope, $\times 600$.



The stomata appear optically less dense than the rest of the epidermis and are therefore conspicuous in the light microscope. They are in well-defined rows separated by two to four epidermal cells.

There are (four), five to six (or seven) subsidiary cells forming the stomatal pit. Externally (Pl. 44, fig. 1), the pit is seen to be bounded by a thick raised ring which is in turn separated from the rest of the epidermis by a fairly deep furrow; again here it is the outer limit of this furrow which is formed by the edges of the surrounding epidermal cells of which there are usually one or two more than the number of subsidiary cells. In the light microscope (Pl. 44, fig. 8) the furrow is indicated by the narrow light band just inside the dense ring formed by the surrounding epidermal cells. The guard cell cuticles are fairly thick and therefore generally present in preparations; orientation is random.

Stomata fade out towards the edge of the leaf-sheath and are absent from the leaf itself, the outer surface of which is papillate due to protruding epidermal cells. The adaxial surface of leaf and sheath is strongly papillate (Pl. 44, fig. 3). The adaxial cuticle of the leaf consists of almost square cells, the regular arrangement of which is sometimes disturbed by a ring-like group of cells suggestive of an abortive stoma (Pl. 44, fig. 3, top left). In the sheath, the adaxial cuticle shows a continuous hypodermis.

Discussion and comparison. Specimens belonging to this species may possibly have been included by Schenk (1869) in the material described as *F. hoheneggeri* from the Carpathians. Some of his specimens (e.g. Schenk, pl. 4, figs. 5–7) certainly bear a resemblance to this species. As already stated above and by Reymanówna (1965) and Hlušík (1974), the status of *F. hoheneggeri* is uncertain. However, most of Schenk's specimens appear to be of a kind having more elongated segments with more than one leaf at the node, possibly three. The material described by Remanówna was certainly mixed. Dr. Reymanówna and I have recently re-examined this material and find that the shoots with more elongated segments and with three leaves show certain cuticle differences from those with shorter segments and only one leaf. These latter, on which Remanówna's (1965) description of the cuticle was based, are regarded as identical to the Portuguese specimens described here and also to material from the Wealden of England which Dr. Watson and I are at present investigating. Dr. Watson has recently re-examined Fontaine's type material of

EXPLANATION OF PLATE 45

?*Frenelopsis occidentalis* Heer, from Almargem (Aptian-Albian).

Fig. 1. Internode cuticle from outside, SEM, $\times 170$.

Fig. 2. Single stoma from outside, showing polygonal mouth of the stomatal pit and papillae in throat, SEM, $\times 1100$.

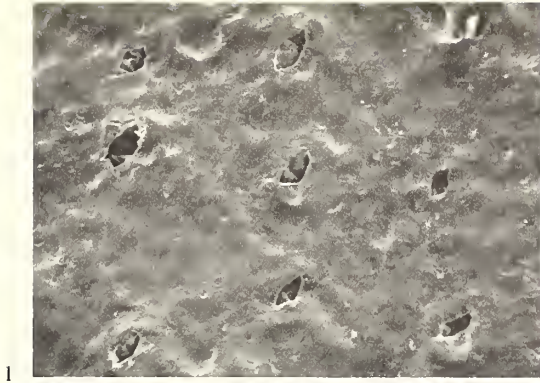
Fig. 3. Internode cuticle from inside, SEM, $\times 170$.

Fig. 4. Stoma from inside, showing subsidiary cells with entrances to the hollow throat papillae, SEM, $\times 800$.

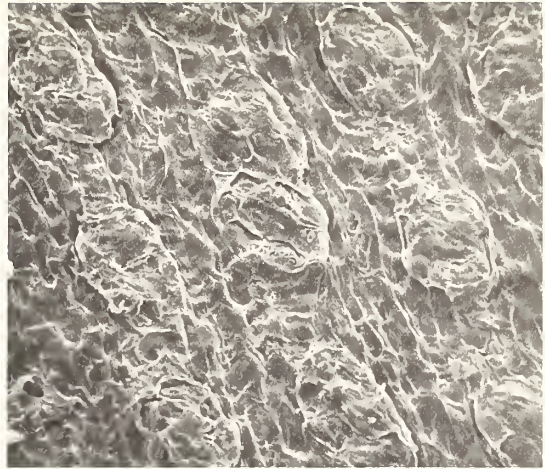
Fig. 5. Section of stoma. Cuticle somewhat compressed, SEM, $\times 1400$.

Fig. 6. Internode cuticle, light microscope, $\times 200$.

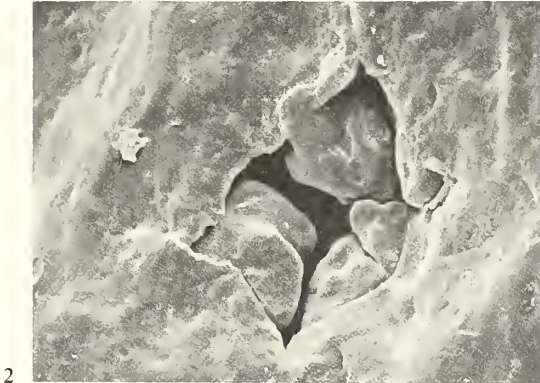
Fig. 7. Stoma, focused through stomatal pit showing the prominent throat papillae, light microscope, $\times 800$.



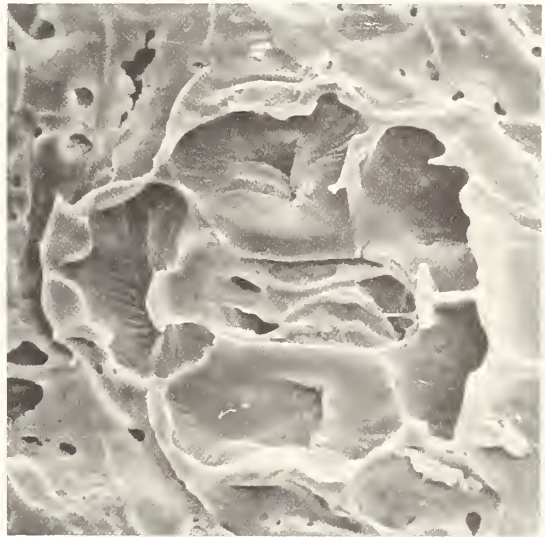
1



3



2



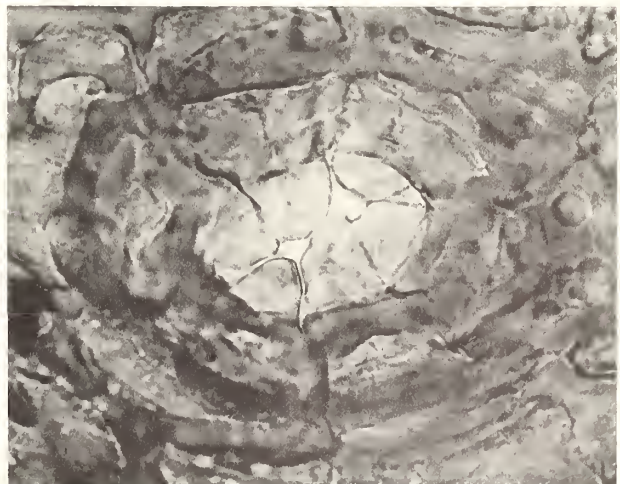
4



5



6



7

F. parceramosa in the Smithsonian Institution and has concluded that it is identical to the English material. She will shortly publish an emended diagnosis of the species.

Variations, however, do occur. The variation within the Portuguese material in the 'open' or 'closed' nature of the leaf-sheath has also been noted by Watson (1964) in material from England. No papillae have been observed extending from the raised ring around the mouth of the stomatal pit in the Portuguese specimens (though the cuticles of only two individual segments have been examined). Papillae are generally present in material from elsewhere, though they may be absent from some English material.

Watson (1974) has proposed the name *Manica* for *Frenelopsis*-like conifers with spirally arranged leaves. Certainly, among modern conifers, such a difference would be regarded as fundamental and meriting generic distinction. Accordingly, I am, for the present, using this name. However, the resemblances in morphology and cuticle characters among these fossil conifers, regardless of phyllotaxy, are strong and when more information concerning the other parts of the plants becomes available, it is possible that the difference in phyllotaxy may no longer provide sufficient grounds for generic separation.

Oishi (1940) recorded this species from Korea, but his records cannot be accepted on the basis of his description which gives no anatomical detail.

Genus ?*Frenelopsis* Schenk
? *Frenelopsis occidentalis* Heer

1881 *Frenelopsis occidentalis* Heer, p. 21; pl. 12, figs. 3b, 4-7.

1946 (pro parte) *Frenelopsis hoheneggeri* (Ettingshausen): Romariz, p. 143; pl. 1, figs. 1-3.

1948 *Frenelopsis hoheneggeri* (Ettingshausen): Teixeira, p. 55; pl. 14, fig. 4.

Locality. Vale de Almargem, between Vale de Figuera and Rio de Sapos, near Almargem, Estremadura, Portugal.

Horizon. Aptian-Albian.

Emended diagnosis. Branching segmented shoots up to 4 mm broad. Segments up to four times longer than broad.

Cuticle of internode up to 60 μm in total thickness with the outer periclinal walls of the epidermis about 25 μm thick. Inner periclinal walls almost continuously cutinized except for small perforations (Pl. 45, figs. 3, 4). Anticlinal walls of hypodermis slightly cutinized.

Epidermal cells in longitudinal rows, isodiametric or up to twice as long as wide, 15-25 μm wide with anticlinal walls about 6 μm thick.

Stomata arranged in longitudinal rows and optically slightly denser than the rest of the epidermis (Pl. 45, fig. 6). Subsidiary cells, five to six. As seen from the outside (Pl. 45, fig. 1), mouth of stomatal pits flush with general cuticle surface or slightly raised. Pit mouth irregularly polygonal in shape, the number of sides equalling the number of subsidiary cells. Papillae in the throat of the pit equalling the number of subsidiary cells, massive and obscuring the guard cells from above (Pl. 45, figs. 2, 5). Guard-cell cuticles rather thin, but commonly surviving maceration. Stomata irregularly orientated, but with some tendency to be parallel in a given area of cuticle.

Further description and discussion. Heer (1881) originally described his material as coming from a different locality (Vale de Lobos) but Choffat (1894) gave reason for believing that it was from Almargem. This was accepted by Teixeira (1948) and Romariz (1946) who regarded the material as Heer's holotype of *F. occidentalis*. I therefore use this name. The single block apparently representing Heer's holotype bears a number of broken shoots and isolated segments. Much of the compressed material has peeled off leaving only impressions. Unfortunately it has not been possible to determine the leaf arrangement and for this reason the generic name must be regarded as tentative.

The specimen, together with those from Olhos Amerelos which I have identified as *Manica parceramosa*, was identified as *F. hoheneggeri* (Ettingshausen) by Romariz. However, although the material from Almargem is fragmentary and has not allowed a very full description, the cuticle is well preserved and provides evidence that it is probably distinct. The most notable differences are the much greater thickness of the cuticle, the more strongly cutinized hypodermis, and stomata differing in a number of details. I know of no other species of *Frenelopsis* with a similar cuticle but the form described as '*Frenelopsis* sp.' by Hlušík (1974) from Štramberk (?Hauterivian) shows some resemblance.

Other records from Portugal. Teixeira (1948) records *Frenelopsis* from several other Cretaceous localities. Some of these specimens I was able to examine in Lisbon, but in none is the preservation good enough for cuticle preparations and accurate identification. *F. leptoclada* Saporta (1894) from the Aptian of Caixaria and also from the Valanginian of San Sebastian in Spain, is based on poor impressions only and cannot therefore be characterized in any worthwhile way.

Another species, probably new, having two opposite leaves at each node, from Sesimbra (Hauterivian or Barremian) is currently being investigated by Dr. J. Pais, University of Lisbon.

Acknowledgements. I am grateful to Dr. Moitino de Almeida, Director of the Museum of the Serviços Geológicos de Portugal, for the help and facilities he extended to me during my visit to Lisbon. I also gratefully acknowledge the grant from the Central Research Fund of London University which made my visit to Lisbon possible. My thanks are also due to Dr. J. Pais, University of Lisbon, for supplying me with information on the Portuguese Cretaceous. The SEM in the Botany Department, Imperial College, was obtained on a grant from the Science Research Council.

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OSTRACOD ASSEMBLAGES AND THE DEPOSITIONAL ENVIRONMENTS OF THE HEADON, OSBORNE, AND BEMBRIDGE BEDS (UPPER EOCENE) OF THE HAMPSHIRE BASIN

by M. C. KEEN

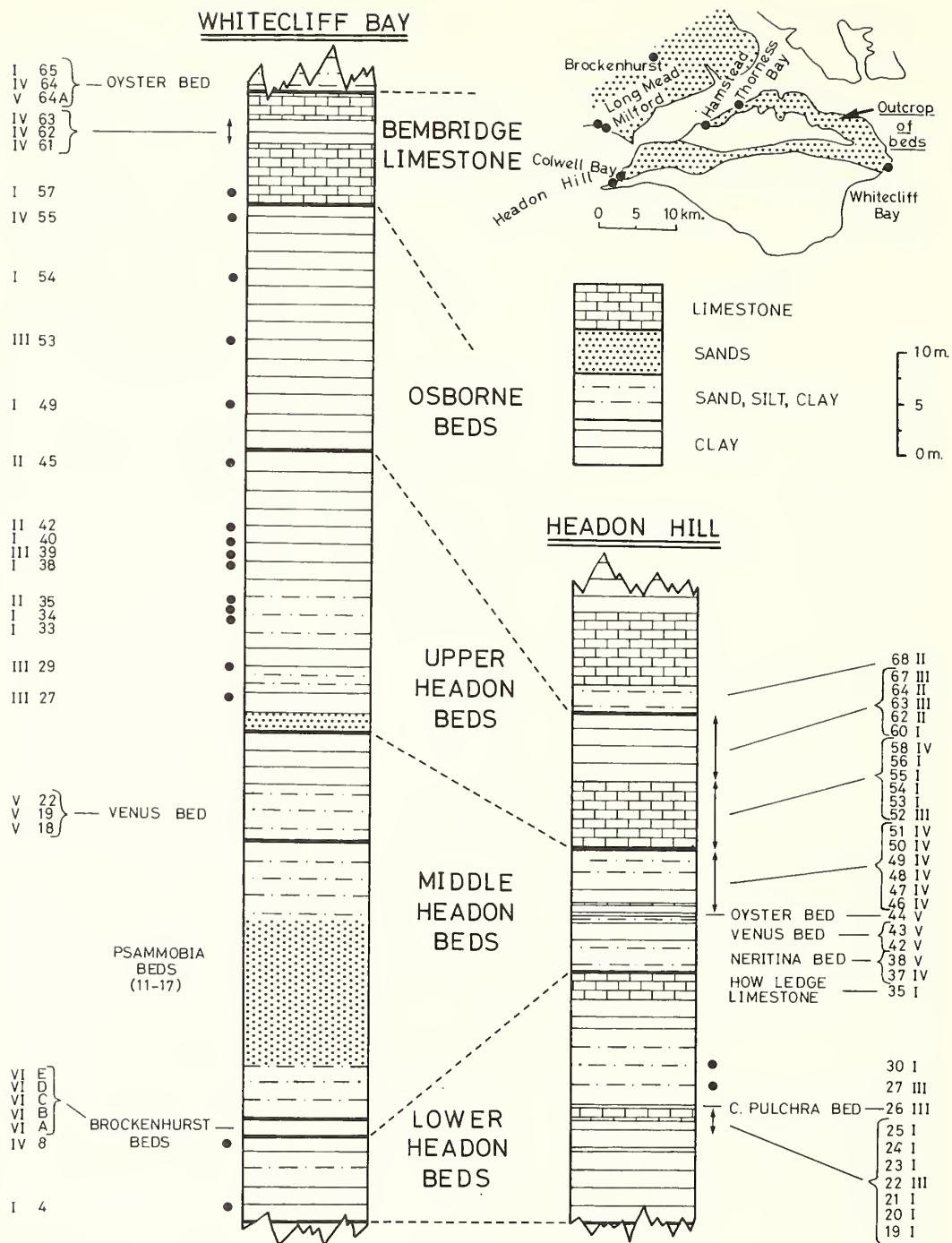
ABSTRACT. Six ostracod assemblages have been recognized from the Headon-Bembridge Beds of the Hampshire Basin by the use of cluster analysis employing Jaccard and Dice Coefficients. They are thought to be salinity controlled and are comparable with Recent ostracod assemblages. Two are believed to represent a freshwater environment (0–3‰ salinity), the first characterized by *Candona* and *Cypridopsis*, the second by *Moenocypris*. Three are believed to represent brackish environments, characterized by *Cytheromorpha* (3–9‰), *Neocyprideis* (9.0–16.5‰), and *Haplocytheridea* (16.5–35.0‰). The sixth assemblage is believed to represent a truly marine environment. Evidence for post-mortem movement of valves and for mixed assemblages is examined. The autecology of *N. cobwellensis* (Jones) is studied, especially the relationship between salinity and size and the development of nodes; variation in carapace ornament is believed to be related to CaCO₃ content of the water. Seven new species and two new subspecies are described.

THE 'Tertiary Fluvio-marine Formation' of Hampshire and the Isle of Wight has attracted the attention of many geologists interested in ancient environments. Amongst the early workers the most outstanding was Edward Forbes, who recognized the freshwater, estuarine, and marine nature of the deposits in his classic work of 1856. In more recent years palaeoecological aspects have been investigated by Bhatia (1957) and Murray and Wright (1974) with Foraminifera; Daley (1972, 1973) on the molluscan assemblages of the Bembridge Beds; Edwards (1967) using the total fauna; and Haskins (1971c) and Keen (1972a) with ostracods.

The ostracods are particularly suited for an investigation of these deposits because of their wide environmental range. Recent years have seen a vast increase in ecological data on living ostracods, so there is now a firm foundation for palaeoecological studies. The taxonomy of these upper Eocene species is also in a reasonably healthy state due to the work of Jones (1856, 1857), Jones and Sherborn (1889), Haskins (1968a–1971b), and Keen (1972a, b, 1973a, b). Haskins (1971c) used ostracods to determine the depositional environments of the Palaeogene of the Isle of Wight, recognizing freshwater, brackish, and marine assemblages in the Headon-Bembridge Beds. Six assemblages are recognized herein, probably essentially salinity controlled. They are comparable with Recent ostracod assemblages, in particular with those recorded from lagoons bordering the Gulf of Mexico.

The horizons studied (text-fig. 1) are the Headon and Osborne Beds, Bembridge Limestone, Bembridge Oyster Bed, and Bembridge Marls. Sampling details for the two main sections, Headon Hill and Whitecliff Bay, are shown in text-fig. 1.

The age of the deposits remains controversial. The base of the Middle Headon Beds has traditionally been regarded by British palaeontologists as the base of the



TEXT-FIG. 1. Sections at Headon Hill and Whitecliff Bay, showing the positions of ostracod-bearing samples; arabic numerals indicate sample number, roman numerals the assemblage to which they belong.

Oligocene, so they have been placed into the Lattorfian, the basal Oligocene stage. Others have placed the boundary at a higher position, often drawing the base of the Oligocene at the base of the Hamstead Beds. This is the view adopted here, so the Headon-Bembridge Beds are regarded as being of late Eocene age. Edwards (1971) gives a full bibliography.

The area of sedimentation was probably a restricted basin bounded by the Ports-down uplift to the north and the Brixton-Sandown uplift to the south. An eastward-flowing river system emptied into this, with the open sea lying to the east and south-east. The sea sometimes penetrated the embayment, giving rise to lagoonal and marine conditions. Evidence of contemporary earth movements has been deduced by Daley and Edwards (1971).

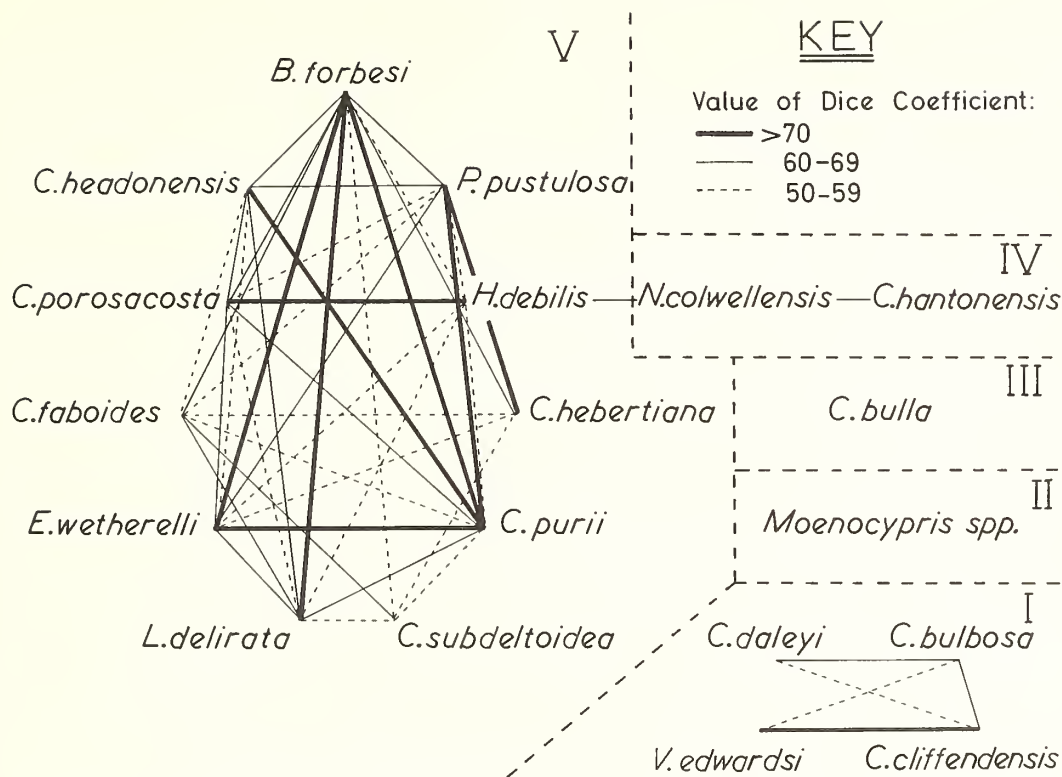
METHODS

One hundred and seventy-six samples were examined, of which ninety-one yielded ostracods. It had originally been decided to count the number of specimens of each species per unit volume of unwashed sediment, but this had to be abandoned as impractical. Some samples yielded several hundred specimens within a short period of time, while others needed several hours in order to find a dozen or so specimens. While it is possible to average out the number of specimens present to a standard unit volume, this practice was not followed because of the great discrepancies between the size of the final samples. The problem may not be too important, however, since the rate of sedimentation is unknown, and volume for volume comparisons may not have much significance; for example, does a high frequency of valves indicate slow deposition of sediment or dense populations? Secondly, the assemblages have been determined by using cluster analysis, which requires the recording of the presence or absence of a species in a particular sample. Thus the main consideration is whether a large enough sample has been examined to record all the species present. Kornicker (1965) has indicated that a sample of 300 specimens yields most species present, while even 150 approaches the actual number. These numbers were readily available for the mesohaline and polyhaline assemblages, but difficult to obtain for the freshwater ostracods, and so this criterion was waived for the latter. Table 1 shows the number of specimens examined in assemblages III, IV, and V.

Cluster analysis is now a fairly standard technique, and various correlation coefficients have been used for determining ostracod assemblages (Kaesler 1966; Carbonnel 1969; and Cheetham and Hazel 1969). The computer program used in this study is that given by Bonham-Carter (1967). Clustering is by the unweighted pair-group method. In the analysis of the data only the common species were considered, defined as those present in five or more samples, and representing at least 3% of the fauna in each sample; nineteen species fall into this category. The reason for eliminating the rare species is that their presence or absence in a sample is much more a matter of chance than for the common species. The results are presented in two forms. Text-fig. 2 is an R-mode analysis using the Dice Coefficient, presented as a constellation diagram, and using simple absence/presence data. The five assemblages are shown as being distinct more graphically than by using a dendrogram. The species of Assemblage V form a large and well-defined cluster with high

TABLE 1. Composition of samples belonging to Assemblages III, IV, and V. N = number of individuals; figures for genera indicate percentage occurrence. Note that, because only the common genera have been used, the percentages do not always total 100. Also note some anomalies that occur due to the clustering method; for example, WB8 with 67% *Neocyprideis* belongs to Assemblage III rather than IV, while BC5 with only 32% *Neocyprideis* belongs to Assemblage IV: this is because of the presence of a third genus, *Cladarocythere* in BC5. Note also the increase in diversity from Assemblage III, through IV, to Assemblage V.

SAMPLE	N	CYTHROMORPHA	NEOCYPRIDEIS	CLADAROCYTHERE	HAPLOCYTHEREIDEA	BRADLEYA	CLITHROCYTHEREIDEA	CYAMOCYTHEREIDEA	CYTHERETTA	EOCYTHEROPTERON	LEGUMINOCYTHEREIS	PTERYGOCYTHEREIS	ASSEMBLAGE
HH 22 HH 26 WB 8 WB 27 WB 29 WB 39 WB 53 HHCP 6 HHCP 13	112 103 108 55 96 31 95 306 77	50 99 33 100 95 65 89 83 50	50 1 67 3 33 11 6										III
HH 37 HH 47 HH 48 HH 50 HH 51 HH 58 CB 6 BC 5 BC 8 WB 63 WB 64 NHH 1 NHH 3	337 398 438 218 85 287 99 96 173 61 53 183 66	26 1 1 63 2 2	60 35 77 80 69 82 58 32 100 96 97 56 97	13 5 10 8 12 17 1 4 22	1 25 6 6 2 2 22	 2 	 1 19 	 1 19 	 8 8 	 8 8 	 1 	IV	
HH 38 HH 42 HH 43 HH 44 CB 1 CB 2 CB 4 CB 5 MF 1 MF 2 BR 3 WB 18 WB 19 WB 22 WB 64a Base VB Mid VB Top VB	115 200 348 403 111 86 813 147 242 173 113 160 175 120 68 132 91 549	31 2 2 1 1 1 1 5 4 14 1 2 1 1 1	10 8 4 2 7 5 5 2 12 5 6	1 1 1 1 1	64 55 29 62 39 54 57 70 11 13 29 55 54 40 85 24 31 31	1 8 3 3 3 6 1 7 10 2 3 15 9 9	7 16 1 2 1 6 1 7 3 2 2 9 4	4 10 16 5 15 8 24 21 15 10 1 1 3 6 5	2 4 2 2 6 3 2 1 1 5 13 10 1 1 1 1	1 4 1 10 3 2 3 3 5 2 1 1 3	2 2 6 1 2 1 1 8 1 7 2 2 1	V	

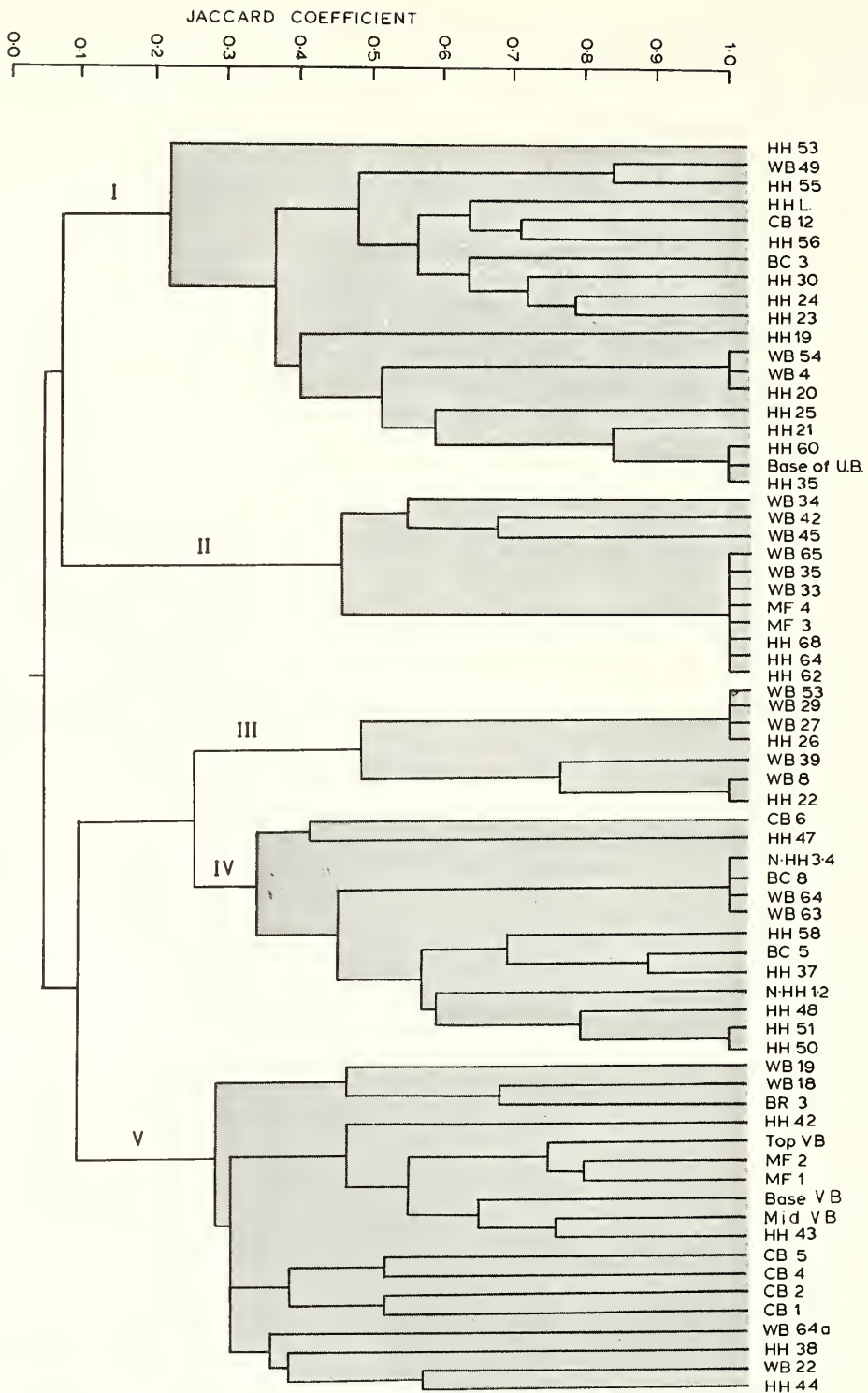


TEXT-FIG. 2. Constellation diagram showing the level of association between the nineteen common species. This is an R-mode analysis using the Dice Coefficient of correlation. Roman numerals indicate the five assemblages which can be recognized.

correlation values between one another, indicating that they frequently occur together. Only one species, *Haplocytheridea debilis*, has a significant correlation with a species belonging to another assemblage. Text-fig. 3 is a Q-mode analysis using the Jaccard Coefficient, presented as a dendrogram, but the species here are divided into absent (< 3%), present (3-25%), and abundant (> 25%) for analysis. In text-fig. 4 the assemblages are shown, together with rare species assigned to them, and with suggested salinities.

OSTRACOD ASSEMBLAGES

The assemblages recognized here are biofacies, i.e. groups of fossils frequently occurring together, and assumed to have had similar environmental requirements. The first part of the definition is supported by the statistical results, the second is deduced by comparison with living relatives. The environment is thought to be the primary control, interrelationships between organisms being secondary. The distribution of individual species differ, giving overlap between some of the assemblages. This is the case with modern marine communities, and is to be expected if



TEXT-FIG. 3. Dendrogram of Q-mode analysis using the Jaccard Coefficient of correlation.
For locality details see Appendix.

the environmental needs of the species within a community are not exactly identical. In this study, overlap is particularly apparent with the brackish water assemblages, where there is almost complete gradation from one assemblage to another, while within assemblages some species are more widespread than others.

The trophic role of ostracods has never been studied in any detail, although they are known to be predominantly scavengers, with some herbivores. They do not seem to be the specific prey of any animals, apart perhaps from the young stages of some boring gastropods, being eaten by benthonic suspension feeders and nektonic filter feeders. Shelter is important for many ostracods, and this can be provided by vegetation or animals such as bryozoans; other ostracods live interstitially and so are independent even of this. Therefore it seems reasonable to consider the environment as the primary control, and the presence of other organisms as secondary. Comparison with living ostracods suggests that there was no interdependence between the ostracods themselves. Following from this, it appears justifiable to consider the ostracods on their own, without detailed consideration of the other phyla present.

Once the assemblages have been recognized, there are other problems to consider. Within any over-all environment there will be different microenvironments; as mentioned above, some ostracods would have lived interstitially, others crawled over the bottom sediment, some lived amongst the weed, others swam amongst it. On death, all of these will be found in the same sediment, giving a single assemblage. It is possible to recognize some of these life styles amongst the freshwater ostracods by comparison with living relatives (Keen 1975), but generally this is not so. However, even with Recent ostracods it is usually impossible to be more precise. Transportation after death is another factor to consider, and is discussed in more detail below. However, the assemblages are thought to represent the fossilized remnants of living communities, and as such, approach the ideal of a palaeontologically defined biocoenosis. This does not mean that no movement occurred after death, but it does imply that such movement was of a limited amount. Individual cases of mixed assemblages are discussed in the relevant sections below.

One final problem remains to be considered. As will be seen from the following discussion, many of the deposits are regarded as lagoonal. By comparison with modern lagoons, sedimentation would have been slow, but rapid changes in environmental conditions could be expected. It is therefore possible that the samples have mixed more than one environment since they were collected from a vertical thickness of about 6 cm. In order to test this idea, three horizons were resampled in detail. Firstly, a small thickness of sediment was sampled in the field using a trowel; a minimum thickness of 2–3 cm could be collected in this way. A second method was to use an aluminium tray, 60 cm long, 5 cm deep, and 10 cm wide which was pressed into a carefully trimmed section, and a spade used to cut it out. In this way a complete section 60 cm long remained in the tray. Top and bottom were marked on the tray, and then it was wrapped in polythene to retain the moisture of the sediment. The sample was examined in the laboratory. Using this method it was possible to examine 0.5–1.0 cm thicknesses of sediment. Thus, in addition to the 176 samples already mentioned, a further fifty-three samples were examined in detail. However, the latter were not used in the statistics because they were from selected horizons and would have heavily weighted the results: e.g. there would have been another thirty

samples of Assemblage V from only 50 cm of sediment, which is out of all proportion to sampling from other horizons. The results obtained from these additional samples are discussed further in the relevant sections below. The most important conclusion, however, is that the original samples are perfectly adequate for this study.

FRESHWATER OSTRACOD ASSEMBLAGES

Two distinct freshwater assemblages which can be recognized have been dealt with in greater detail by Keen (1975). Both can be recognized in the Hamstead Beds (Keen 1972a), and are also recorded from the Palaeogene of the Paris Basin, Rhine Valley, Mainz Basin, and Hesse.

Assemblage I. The *Candona-Cypridopsis* Assemblage. This is characterized by *Candona* spp. and *Cypridopsis* spp., with *Virgatocypris edwardsi* sp. nov. and *Cypria dorsalta* Malz and Moayedpour. Associated molluscs are *Galba* and *Planorbina*, with rare *Melanopsis*. *Chara* is usually abundant and seeds of waterplants often present. The sediment is a grey-green clay, a black carbonaceous clay, or a buff limestone. *V. edwardsi*, *Candona cliffendensis* sp. nov., and *Cypridopsis bulbosa* (Haskins) have a significant relationship with limestones; using a χ^2 test p was found to be 0.001, 0.005, and 0.03 respectively (Keen 1975). The first two species are more or less restricted to limestones, but *C. bulbosa* has a much wider distribution. Only one assemblage is recognized, although it could be divided into two sub-assemblages, i.e. one from limestones, and the other from clays.

Assemblage II. The *Moenocypris* Assemblage. *Moenocypris* is the only ostracod belonging here. Two species are present, *M. sherborni* Keen in the Lower Headon Beds, and its descendant *M. reidi* Keen in the Upper Headon and Osborne Beds. *Moenocypris* is an extinct genus, but there is little doubt that it inhabited freshwater (Keen 1975). The samples come from grey clays with common *Viviparus*, *Melanopsis*, and *Unio*, rarer *Potamaelis* (Fam. Melaniidae); serpulids (sometimes present); and *Chara* (rare). Seeds of waterplants are often abundant.

There is little doubt that these two assemblages inhabited freshwater. The difficulty is in accounting for the existence of two distinct assemblages. A certain amount of mixing is indicated by the coefficients of correlation; *Moenocypris-Cypridopsis bulbosa* is 17, with lesser values between other members of Assemblage I and *Moenocypris*. Such values can be explained by post-mortem movement. The controlling factor is believed to be the depth of water. Daley (1972) has already discussed this with regard to the molluscan assemblages, and Keen (1975) concerning the ostracods, so it is only necessary to give the conclusions here. The *Candona-Cypridopsis* Assemblage is thought to have characterized lake margins or shallow lakes up to about 1 m or so in depth. This would coincide with the upper infra littoral zone, or zone of emergent waterplants. The water would have been still or slowly moving, with an alkaline pH (~ 8) and a positive Eh. The *Moenocypris* Assemblage is thought to have characterized deeper water (2–15 m?) coinciding with the lower infra littoral zone, or zone of submerged waterplants, or bare muddy bottoms. The water would have been still, with poor circulation, an alkaline pH, and the bottom sediments probably had a negative Eh.

BRACKISH WATER ASSEMBLAGES

Three brackish water assemblages have been recognized, ranging from a low salinity assemblage, through mesohaline, to polyhaline.

Assemblage III. The *Cytheromorpha* Assemblage. This is characterized by *C. bulla* Haskins; other ostracods found here are discussed below. This assemblage is more common than indicated on the dendrogram, but several samples could not be included in the analysis because they contained too few specimens. It is found in two differing sediments: the first is a grey clay with abundant shells of the bivalve *Potamomya plana* J. Sowerby, subordinate *Melanopsis*, *Theodoxus*, and *Corbicula*, with rare *Viviparus*, *Galba*, and *Planorbina*; the second is a green clay with few or no molluscs. *Cytheromorpha* is found at the present day in salinities ranging from 0–35‰. It is characteristic of brackish waters. Wagner (1957) records it from lower mesohaline (2–10‰); Puri (1968) from an estuarine environment (0–26‰); Swain (1955) from typical Texan bays (2–10‰); Curtis (1960) as being typical of 'closed shallow lagoons, away from fluvial influence and with little marine influence'. The living molluscs are typical of subtropical rivers and estuaries. The presence of rare *Galba*, *Planorbina*, and *Viviparus* suggest a fluvial influence, although these shells are probably allochthonous. It is usually assumed that the poorest brackish water assemblages, in terms of number of species, are found in salinities below 9‰. This assemblage has the least number of species, and, together with the known range of living *Cytheromorpha*, is taken to indicate a salinity of 3–9‰.

Assemblage IV. The *Neocyprideis* Assemblage. *N. colwellensis* (Jones) is the dominant ostracod of this assemblage, although the actual composition varies between samples. *Cladarocythere* spp. are commonly present, *Cytheromorpha bulla* and *Haplocytheridea debilis* (Jones) more rarely. *Bradleya favosa* Haskins is assigned to this assemblage, although as it only occurs four times it was not considered statistically; it is only found in samples dominated by *N. colwellensis*. It is placed in *Bradleya* for convenience, belonging to an undescribed genus; a second species, *B. dolabra* Keen has been described from Oligocene brackish water deposits (Keen 1972a). The sediment is a clay or sandy clay. The molluscan fauna varies; samples with *C. bulla* contain juvenile *Galba*, *Planorbina*, and *Corbicula obovata* (J. Sowerby); a distinctive fauna from the Middle Headon Beds consists of *Batillaria ventricosa* (J. Sowerby), *Potamides vagus* (Solander), *Globularia grosa* (Deshayes), and rare *Ostrea*: *B. favosa* and *H. debilis* are found with this second association. The commonest molluscs, however, are *C. obovata* and *P. vagus*. The Foraminifera *Quinqueloculina* is sometimes present.

Neocyprideis is an extinct genus, but is closely related to the living *Cyprideis*, which some believe to be its descendant. The latter is probably the most typical brackish water ostracod; its ecology has been fully described by Sandberg (1964): it is found in freshwater, is common in mesohaline waters, rarer in polyhaline and euhaline waters, but abundant in hypersaline conditions. Its greatest development is in mesohaline salinities. It usually inhabits relatively quiet water, such as creeks bordering estuaries, lagoons, or brackish 'ponds' close to the sea (Whittaker, pers. comm. 1975). It is a bottom crawler, or burrower, feeding on organic matter in the

sediment. In low salinities, *Cyprideis* develops nodes on its shell, and may increase in size; these factors are studied below. Assemblage IV is taken to represent salinities of 9.0–16.5‰. The other characteristic ostracod of this assemblage is *Cladarocythere hantonensis*. This extinct genus is found in Eocene and Oligocene brackish water sediments. Its ecology can only be derived from associated faunal elements, and there is some indication that different species had differing salinity preferences. *C. hantonensis* is taken to have inhabited upper mesohaline and polyhaline salinities, but *C. apostolescui* (Margerie) has been taken to belong to lower mesohaline salinities in the Paris Basin (Keen 1971, 1972a). This species is also present in the Hampshire Basin and represents a special assemblage consisting almost entirely of *C. apostolescui*. It is found in the marl immediately below the topmost Bembridge Limestone at Whitecliff Bay, Thorness Bay, and Bouldnor Cliff. Because it occurred in only four samples it could not be included in the cluster analysis, neither could the samples containing it, because the only other ostracod present, *Neocyprideis*, represented less than 3% of the fauna and so counted as 'absent' under the procedure adopted for this study.

Assemblage V. The *Haplocytheridea* Assemblage. This is characterized by *H. debilis*. The sediment is a silty or sandy clay, often with large numbers of *C. obovata* in life positions. Other molluscs include *Sinodia suborbicularis* (Goldfuss), *Ostrea*, *Globularia*, *Nucula*, *Natica*, and a few *Galba* and *Planorbina*. The Foraminifera *Rotalia* and *Quinqueloculina* are commonly present.

Living *Haplocytheridea* are recorded from estuarine and open lagoonal environments, especially along the coast of Texas, Louisiana, and Florida. They are recorded from: depths up to 21 ft, salinity 16–33‰ (Curtis 1960); the Lower Bay subfacies, salinity 10–17‰ (Swain 1955); rocky tide pools of normal marine salinity (Benson in Moore 1961); mangrove swamps and marine environment, salinity 23–40‰ (Benda and Puri 1962); shallow marine waters (Hulings and Puri 1964); lagoonal areas, salinity 10–25‰ (Engel and Swain 1967). Howe (1971) has shown how torose cytherideidae, which includes *Haplocytheridea*, have been used by petroleum geologists to locate ancient shorelines in the Gulf states of America; thus *Haplocytheridea* is regarded as being typical of areas adjacent to the shoreline, usually lagoonal or estuarine, and generally indicating reduced salinities. From this it can be seen that *Haplocytheridea* is typical of polyhaline and marine salinities. The other ostracods present vary from sample to sample, but those with living relatives, i.e. *Cushmanidea*, *Cytheretta*, *Cytherella*, *Paijenborchella*, *Paracytheridea*, *Pterygocythereis*, *Pontocythere*, and *Krithe*, are essentially marine genera, although most can adapt to polyhaline conditions (Swain 1955; Curtis 1960; and especially Puri 1968). Assemblage V is taken to indicate a polyhaline environment, salinity ranging from 16.5 to 35.0‰. The differences between samples is discussed further below. The possibility of hypersaline conditions must be borne in mind. These would have been very temporary, and due to evaporation. There is no geological evidence for permanent high salinities; there are no evaporites, and there is ample evidence of freshwater conditions with many water plants, and lowland vegetation. This contrasts with conditions in the Paris Basin.

THE BROCKENHURST BED

Assemblage VI. The *Hazelina* Assemblage. There were not enough samples from this thin (50–100 cm) horizon to warrant statistical treatment. However, the characteristic fauna suggests that this could be regarded as a separate assemblage. It lacks many of the characteristic polyhaline species of Assemblage V, while the presence of such genera as *Bairdia*, *Hazelina*, and *Idiocythere* suggest truly marine conditions. Molluscs are *Natica*, *Ostrea*, *Modiola*, *Cardium*, *Fusus*, and *Voluta*; solitary corals are recorded; Foraminifera are *Cibicides*, *Rotalia*, *Globigerina*, and *Nonion*.

The paucity of the fauna suggests near-shore, perhaps even sublittoral waters, but of normal marine salinity.

MARSH FACIES

Finally, there is a widespread facies which has not yielded ostracods. It consists of finely laminated clay and sand, sometimes with thin lignitic layers. It is considered to represent a marsh facies. It is especially prominent in the Lower and Upper Headon Beds.

LIFE AND DEATH ASSEMBLAGES

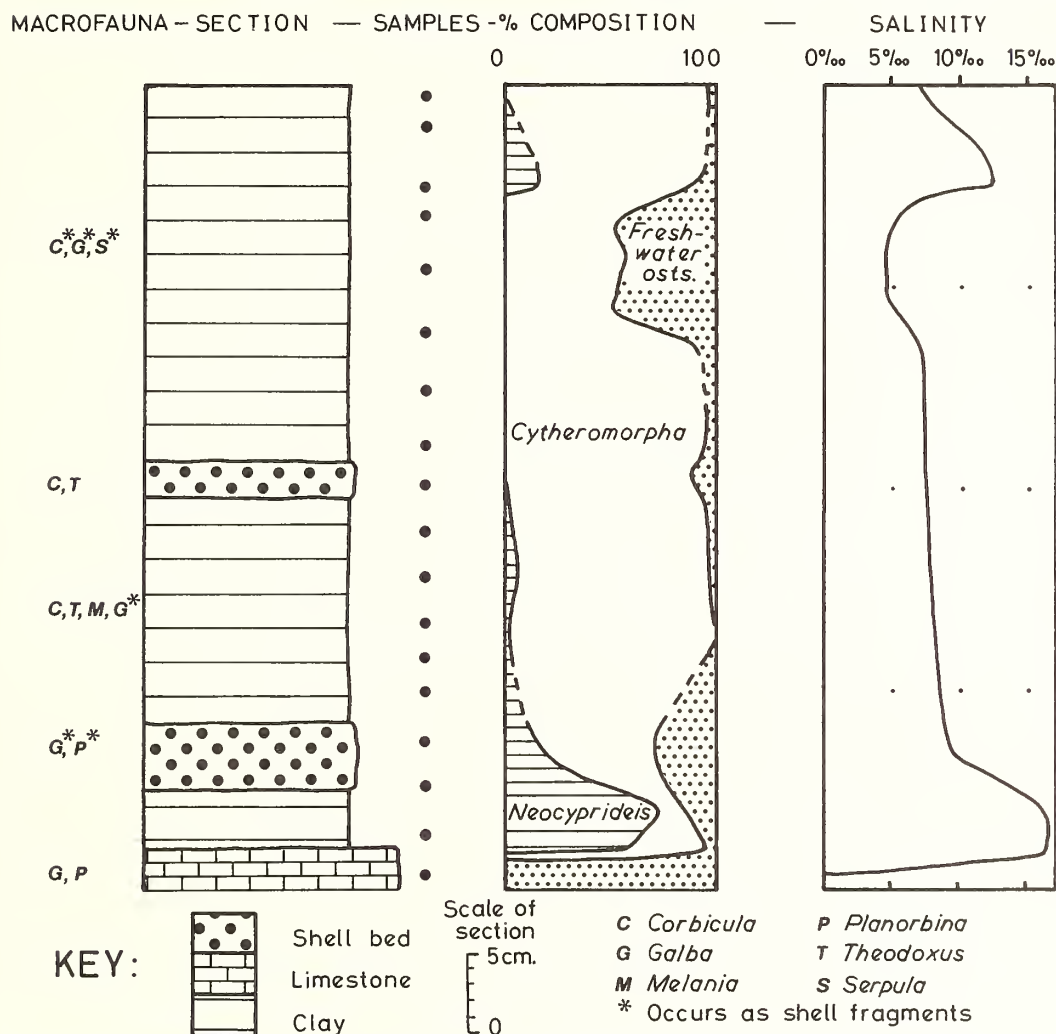
It has been suggested that Assemblages III, IV, and V are salinity controlled and probably formed a gradational sequence. Species which had a broad environmental tolerance probably lived amongst more than one assemblage, while movement of valves after death could lead to mixing of assemblages. *Cytheromorpha bulla*, *Neocyprideis colwellensis*, and *Haplocytheridea debilis* are commonly present in more than one assemblage, so it is worth considering in some detail whether their distribution is due to post-mortem movement or reflects original life habitats. Living members of these genera, as noted above, are adapted to a wide range of salinities, so it is possible that these fossil species might have behaved similarly.

Several criteria have been used to indicate an ostracod biocoenosis: presence of several different moult stages, including adults; presence of carapaces rather than single valves; and equal numbers of each valve. The following example illustrates the use of these, together with stratigraphical succession and faunal composition. In text-fig. 5 a detailed section through the *Cyrena pulchra* Bed (Lower Headon Beds) is shown, with the percentages of *Neocyprideis*, *Cytheromorpha*, and freshwater ostracods from the various samples recorded, and a suggested salinity profile. The section starts in a buff limestone with numerous and well-preserved *Galba* and *Planorbina*. The ostracods belong to Assemblage I, contain many moult stages and adults, few specimens are broken, *Cypridopsis* in particular has many carapaces, and there are approximately equal numbers of each valve of each moult stage. This indicates little post-mortem movement, and so is taken to represent the biocoenosis. Immediately above the limestone, the green clay contains many small fragments of *Galba*; the most abundant ostracod is *Neocyprideis*, with common *Cytheromorpha*, but very rare freshwater ostracods; the second sample is similar. Both of these

SPECIES SUGGESTED SALINITY ‰→	ASSEMBLAGE					
	I	II	III	IV	V	VI
	0-3		3-9	9-16.5	16.5 - 25 - 33	33
<i>Condona cliffensis</i> SP. NOV. <i>Cypridopsis hessani hantonensis</i> SUBSP. NOV. <i>Cyprio dorsalis</i> MALZ & MOAYEDPOUR <i>Cypris</i> sp. <i>Dorwinula</i> sp.	— — — — — — — — — — — — — — — — — — — —					
<i>Condona</i> sp. <i>Strandesio</i> cf. <i>spinosa</i> STCHEPINSKY ⁶ <i>Virgotocypris edwardsi</i> SP. NOV. <i>Virgotocypris</i> sp. ⁶ <i>Condona daley</i> SP. NOV.	— — — — — — — — — — — — — — — — — — — —					
<i>Cypridopsis bulbosa</i> (HASKINS) <i>Maenocypris sherborni</i> KEEN ¹ <i>Maenocypris reidi</i> KEEN ² <i>Cytheromorpha bullo</i> HASKINS ³ <i>Cytheromorpha unisulcata</i> (JONES) ⁴	— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —			
<i>Cytherura pulchra</i> SP. NOV. <i>Neocyprideis colwellensis</i> (JONES) ⁵ <i>Neocyprideis williamsoniana</i> (BOSQUET) ⁶ <i>Cladocythere hantonensis</i> KEEN ¹ <i>Cladocythere apostolescui</i> (MARGARIE) ⁶			— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	
<i>Bradleya favosa</i> HASKINS <i>Paracypris</i> sp. A. <i>Hoplacytherideo debilis</i> (JONES) <i>Clithrocytherideo faboides</i> (BOSQUET) <i>Cushmanideo haskinsi</i> SP. NOV.			— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	
<i>Cushmanideo stintoni</i> SP. NOV. <i>Cushmanideo wightensis</i> SP. NOV. <i>Cyamocytherideo herbertiana</i> (BOSQUET) <i>Cyamocytherideo purii</i> HASKINS <i>Cyamocytherideo subdeltoidea</i> HASKINS				— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	
<i>Bradleya forbesi</i> (JONES & SHERBORN) <i>Cytherella pustulosa</i> KEIJ <i>Cythereilloidea lacunosa</i> HASKINS <i>Cytheretta headonensis</i> HASKINS <i>Cytheretta porosocosta</i> KEEN				— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	
<i>Eocytheropteron wetherelli</i> (JONES) <i>Flexus ludensis</i> KEEN <i>Leguminocythereis cancellosa</i> HASKINS <i>Leguminocythereis delirata</i> (JONES & SHERBORN) <i>Loxoconcha</i> sp.				— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	
<i>Paracytheridea gradata</i> (BOSQUET) <i>Paijenborchella brevicosta</i> HASKINS <i>Pterygocythereis pustulosa</i> HASKINS <i>Schulterideo perforata headonensis</i> SUBSP. NOV. <i>Cytheretta</i> aff. <i>C. stigmose</i> TRIEBEL				— — — — — — — — — — — — — — — — — — — —	— — — — — — — — — — — — — — — — — — — —	
<i>Haplacytheridea montelli</i> KEEN <i>Leguminocythereis</i> cf. <i>L. striatopunctata</i> (ROEMER) <i>Pokornyeella osnabrugensis</i> (LIENENK LAUS) <i>Ruggeria semireticulata</i> HASKINS <i>Krithe bortonensis</i> (JONES)					— — — — — — — — — — — — — — — — — — — —	
<i>Boirdio</i> sp. <i>Cythereello</i> cf. <i>C. compresso</i> (VON MUNSTER) <i>Cythereella</i> sp. <i>Hozelino indigeno</i> MOOS <i>? Idiocythere bortoniana</i> HASKINS <i>Pterygocythereis</i> cf. <i>P. fimbriata</i> (VON MUNSTER)					— —	— —
1 Lower Headon Beds only 2 Upper Headon & Osborne Beds 3 Headon Beds 4 Osborne & Bembridge Beds 5 Headon & Osborne Beds 6 Bembridge Beds						Always present, usually abundant Usually present Rare Present as thanatocoenosis.

TEXT-FIG. 4. Ostracod assemblages from the Headon-Bembridge Beds, with suggested salinities.

ostracods are represented by several different moult stages and contain similar numbers of each valve; these therefore represent the biocoenosis. The freshwater ostracods and molluscs are probably derived. Ascending the succession, *Neocyprideis* declines in numbers and eventually disappears, while *Cytheromorpha*



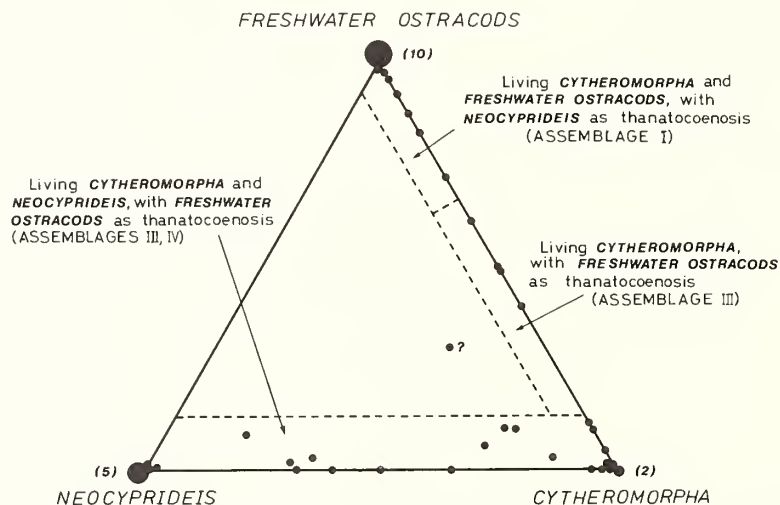
TEXT-FIG. 5. Section through the *Cyrena pulchra* Bed of Headon Hill, showing composition of ostracod fauna and suggested salinity.

becomes dominant. Towards the top the freshwater ostracods become common, forming up to 50% of the samples, but they are mainly represented by broken valves, with very few adults, while the freshwater molluscs are also fragmentary. They therefore represent fluviially transported material and belong to the thanatocoenosis. The section is interpreted as showing a shallow freshwater lake (Assemblage I)

situated near a coastline; the sea breached a barrier some distance away, leading to a rapid rise in salinity as the lake became converted into a lagoon. This caused the death of the freshwater animals and the introduction of a mesohaline fauna (Assemblage IV). The sea connection was short lived, the lagoon began to silt up, and freshwater influence increased (Assemblage III). Towards the top of the section fluvial influence was strong, introducing transported shells into the lagoon. Near the top, the reappearance of *Neocyprideis* and disappearance of the freshwater ostracods indicates another invasion of the sea, although this was not very long lived and the salinity was soon reduced.

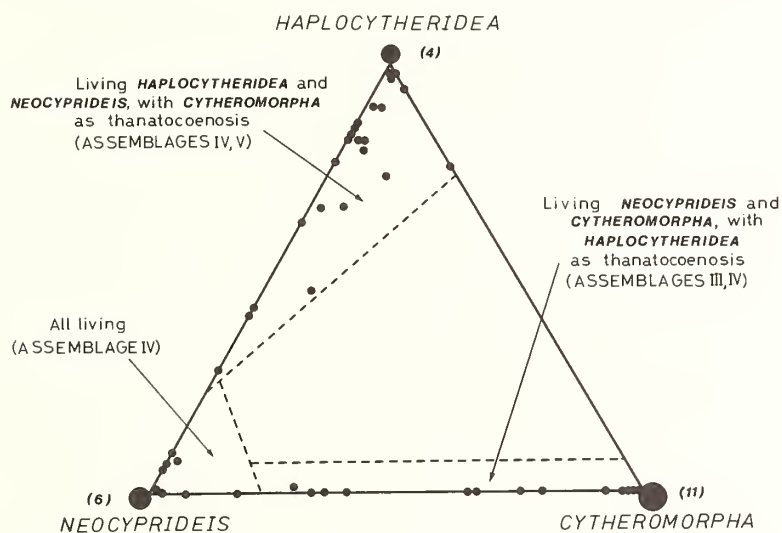
Another method of studying the samples is to regard them in terms of 'end-members' of gradational series. Four ostracod groups can be thought of as 'end members', *Haplocytheridea*, *Neocyprideis*, *Cytheromorpha*, and freshwater ostracods, so that each sample can be described in terms of the percentage occurrence of each of these. *Haplocytheridea* and the freshwater ostracods are almost mutually exclusive so we are left with a series of one, two, or three component samples which can be studied visually by using triangular diagrams. These are given in text-figs. 6 and 7. The first thing to notice, as would be expected, is that the samples do not plot in a random fashion, i.e. there is no scatter of points all over the diagram. Secondly, the samples show a continuous gradation from freshwater $\rightarrow$ *Cytheromorpha $\rightarrow$ *Neocyprideis $\rightarrow$ *Haplocytheridea much as would be expected if the assemblages were controlled by a gradually changing parameter, in this case thought to be salinity.***

The species present in each sample have been examined, using the criteria outlined above, to determine whether they were more probably biocoenosis or thanatocoenosis. It is admitted that the conclusions are relatively subjective, but when plotted on the diagrams they help in giving a consistent interpretation. In text-fig. 6 *C. bulla*, *N. colwellensis*, and freshwater ostracods have been plotted from fifty-one samples



TEXT-FIG. 6. Triangular diagram of samples belonging to Assemblages I-IV showing percentage composition of freshwater ostracods, *Cytheromorpha* and *Neocyprideis*.

excluding samples belonging to Assemblage V. It can be seen that *Neocyprideis* is rarely found in samples dominated by freshwater ostracods: in fact it only occurs once, and then forms only 1% of the fauna; these probably represent valves washed into a freshwater environment. On the other hand, freshwater ostracods are found in many samples dominated by *Cytheromorpha* and/or *Neocyprideis*; these are interpreted as valves carried by rivers into a lagoonal environment. The plots suggest complete gradation along the *Cytheromorpha*-freshwater and *Cytheromorpha*-*Neocyprideis* axes, indicating considerable overlap between living populations of these two sets of ostracods. In the case of *Cytheromorpha* and *Neocyprideis*, the presence of moults and adults, and equal numbers of each valve support this view. In the case of *Cytheromorpha* and the freshwater ostracods the same criteria suggest that *Cytheromorpha* could adapt to virtually freshwater conditions, occasionally forming a minor part of the freshwater biocoenosis; the freshwater ostracods in samples dominated by *Cytheromorpha* seem to belong to the thanatocoenosis.



TEXT-FIG. 7. Triangular diagram of samples belonging to Assemblages III-V showing percentage composition of *Haplocytheridea*, *Neocyprideis*, and *Cytheromorpha*.

In text-fig. 7 similar methods have been used to define the three fields indicated on the diagram. Thus *Cytheromorpha* is regarded as belonging to the thanatocoenosis in samples belonging to Assemblage V. These may represent dead valves carried by currents, or possibly stray animals which endured the increase in salinity, but could not breed. *Neocyprideis* is regarded as a living, breeding, member of the more brackish parts of Assemblage V.

One problem which could distort all of the above conclusions is that of rapidly changing conditions leading to *remanié* contamination. Thus, *Neocyprideis* might be inhabiting a mesohaline lagoon; a rapid rise in salinity could kill it and introduce a polyhaline fauna. With very slow sedimentation these two populations would become mixed. The example of the *Cyrena pulchra* Bed given above shows that

changing conditions can be recognized, at least in some cases, by detailed sampling. The case of *Neocyprideis* in Assemblage V needs some examination because it is often one of the most abundant constituents in samples from Headon Hill and Colwell Bay. With this in mind, the top 60 cm of the Venus Bed at Headon Hill were examined by taking thirty-three samples covering varying thicknesses of between 1 and 3 cm. The lowest 9 cm consisted of green clay, apparently without macrofossils, but containing fairly numerous *Candona*, represented by several different moult stages, some *Cypridopsis* and a few *Virgatocypris*, i.e. Assemblage I. The clay was extensively cut by burrows filled with the overlying sediment, so great care had to be taken to avoid contamination of samples. The overlying bed was a sandy clay, grading upwards into a fine sand, but extremely fossiliferous throughout. The burrows into the freshwater clay indicate that the clay was quite hard before burrowing took place, while the lack of burrows in the overlying sand could be taken as evidence of fairly rapid sedimentation. The burrow infills and the lowest 2 cm of this bed contained ostracods of Assemblage V together with freshwater ostracods, which, because of their preservation, were obviously derived from the underlying clay. The remaining 49 cm contained ostracods of Assemblage V, with *Neocyprideis* evenly distributed throughout. No unusual concentrations of the latter were found, as might be expected if it had only lived at certain times during this interval, and it was always represented by several different moult stages. It could be argued that the changes were so frequent as to destroy any horizons rich in *Neocyprideis*. Against this is the fact that layering of shells is present in the deposits, although bedding is poorly developed.

Secondly, we can consider the likely biology of *Neocyprideis*. If it was similar to *Cyprideis*, it probably had a single breeding season per year. Some support for this is indicated by the moult stages forming discrete groupings (text-fig. 11); ostracods which breed more than once a year do not often show this because those hatched during a warmer period grow faster, but are smaller, giving an almost continuous variation in size. If this was the case, *Neocyprideis* would have needed at least two to three years to establish the viable population indicated by the fossils. It also follows that its presence cannot be explained by seasonal fluctuations, i.e. *Neocyprideis* living at a time of the year when the salinity was lower. Migration may have been involved but seems unlikely by comparison with living *Cyprideis*. The evidence therefore suggests that *Neocyprideis* was a member of Assemblage V.

There is considerable variation between samples belonging to Assemblage V. Certain features are recognizable, however. Nearly all the samples are dominated by *H. debilis*, and *Cytheretta porosacosta* is usually next in abundance. There are notable differences between samples from Whitecliff Bay and those from the west of the Isle of Wight; *Clithrocytheridea*, *Cyamocytheridea*, and *Schuleridea* are rare in the east, but abundant in the west, while *Neocyprideis* is absent in the east. These genera are rather brackish water ones compared with the faunas found in the east. The differences between samples are probably due to differing salinities within the polyhaline range.

MORPHOLOGICAL VARIATION OF *NEOCYPRIDEIS COLWELLENSIS*

Brackish water ostracods show considerable variation in size and ornamentation related to variation in salinity. *N. colwellensis* was examined to see whether such variation offered any help in interpretation of environmental conditions. The results are given in Table 2.

TABLE 2. Distribution of size and nodosity in *Neocyprideis colwellensis* (Jones). Numbers in brackets are the number of measured female left valves; these numbers are low because adults normally form only about 10% of the preserved population. For discussion see text; for locality details see Appendix.

SAMPLE	NUMBER OF SPECIMENS	MEAN LENGTH ♀ L	ASSEMBLAGE	NODOSITY
WB 63 HH 58 CB 1 BR 1 VB 18 HHCP 2 NHH 4	58 (2) 240 (5) 2 (2) 6 (1) 5 (5) 104 (12) 66 (5)	.87 .85 .84 .84 .80 .78 .75	IV IV V V V IV IV	ADULTS AND INSTARS SMOOTH
HH 44 HH 42 HH 22 MF 1 NHH 3	16 (3) 20 (1) 56 (3) 17 (2) 65 (3)	.89 .87 .85 .84 .77	V V IV V IV	ADULTS SMOOTH, OCCASIONAL NODOSE INSTARS
HH 51 NHH 2 HH 47 NHH 1 HH 48	57 (5) 64 (2) 140 (10) 101 (11) 337 (21)	.80 .80 .79 .79 .76	IV IV IV IV IV	OCCASIONAL NODOSE ADULTS, MOST INSTARS NODOSE
HH 37	202 (13)	.77	IV	ALL COMMONLY NODOSE

Noding

Cyprideis and related genera develop hollow nodes or tubercles as a response to decreasing salinities. A salinity of 5‰ is often quoted as the figure below which noded forms become dominant. Vesper (1972a) has confirmed this in a detailed study of *C. torosa* (Jones); he found occasional noded adults in salinities up to 14‰, but between 6‰ and 2‰ they dramatically increased to form 85% of the population. The nodes are genetically controlled because they develop in specific places; Kilenyi (1972) believes that selection operates in favour of noded forms as the salinity decreases, eventually giving balanced polymorphism. With regard to *N. colwellensis*, only one sample (HH37) contains a high proportion of noded adults; this sample is intermediate between Assemblages III and IV. Noded adults are rare or absent in all other samples, although some samples of Assemblage IV have

common noded juveniles. Thus, if *N. colwellensis* reacted to decreasing salinity in the same way as *C. torosa*, it was never found in salinities below 5‰, lending support to the salinity suggested for Assemblage IV.

Size

There is some controversy over the relationship between size and salinity in ostracods; a recent review can be found in Van Harten (1975). Barker (1963) indicated a decrease in size with decreasing salinity in the ostracods *Leptocythere* and *Loxiconcha*. These were marine forms adapting to an estuarine environment; with euryhaline species Hartmann (*in Keen* 1971) stated that size is independent of salinity. Vesper (1972*b*) appeared to confirm this in a study of *C. torosa*, suggesting a positive relationship between size and food supply. However, Van Harten (1975) found a significant negative correlation between size and salinity in this species, but the change was not gradual because populations from salinities below 5‰ were markedly larger than those from above. In this respect the increase in size appears to behave similarly to the increase in nodosity. *N. colwellensis* shows no clear relationship between size and suggested salinity. In general, specimens from Assemblage V fall into the upper part of the size range while those from Assemblage IV occur throughout the range. This, as with nodding, may be because *N. colwellensis* never inhabited salinities below 5‰, in which case the variation in size may be positively related to food supply.

Haskins (1969) observed that the largest specimens came from a sample collected immediately above the Bembridge Limestone, and postulated that this may have been related to an abundance of calcium carbonate in the water. Applying this to the present study this hypothesis seems unlikely. The largest specimens do come from lime-rich sediments, but so do relatively small ones; and the only pure limestone (HH58) yields individuals of about average size. Finally, although perhaps not strictly relevant to a brackish water animal, Reymont and Brannstrom (1963) found that in laboratory studies of the freshwater ostracod *Cypridopsis* those reared in abnormally high lime-rich waters or stagnant waters grew to a smaller size than those from the normal environment.

Variation in ornamentation

Specimens of *N. colwellensis* may be smooth or punctate. Five samples contained smooth forms, all coming from calcareous horizons. It is postulated that smooth forms are phenotypes which developed in lime-rich waters.

LIVING CONDITIONS OF THE BRACKISH WATER ASSEMBLAGES

The salinities indicated above are found in both estuarine and lagoonal areas and it is often difficult to differentiate between these in the geological record. Estuaries are high-energy environments with a great deal of transportation of material both from the sea and from the river, which leads to mixing of faunas. Freshwater faunas give way to brackish, which in turn give way to marine faunas; freshwater shells may be found throughout. This, in fact, has been found to be the case in the Headon Beds. Lagoons and bays have a more restricted access to the sea and are generally

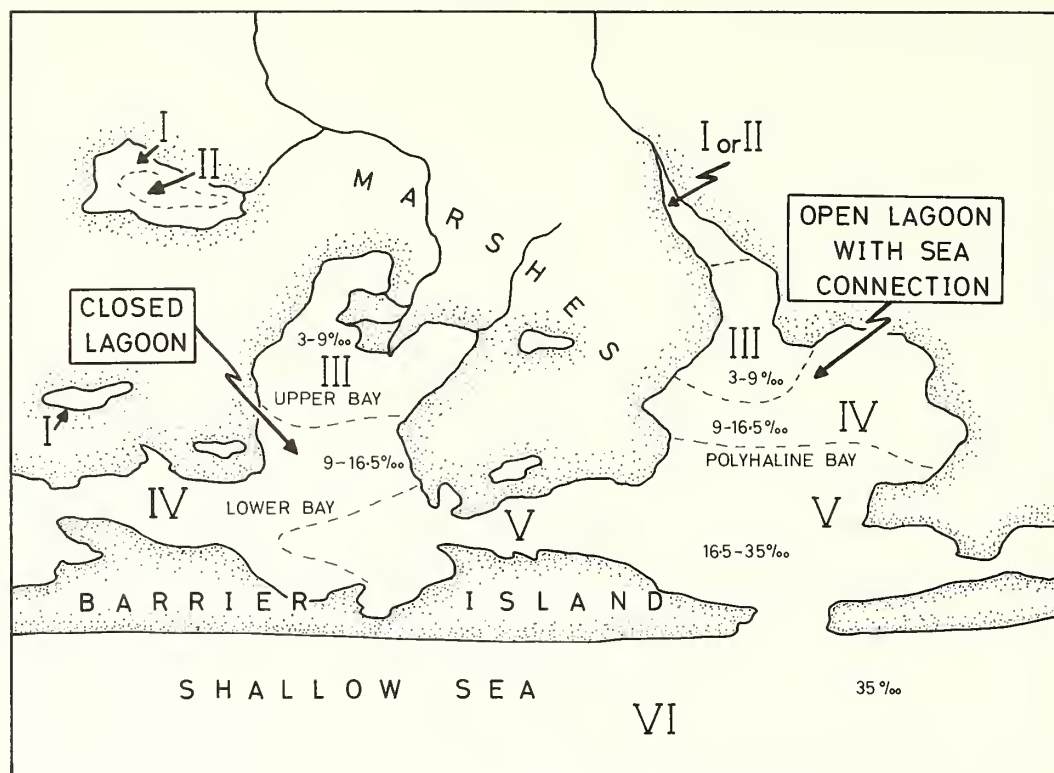
bodies of very shallow water with gradual salinity changes between lagoons. The fauna may give some indication as to which of these conditions prevailed. In the polyhaline part of modern estuaries the marine element is often represented by large numbers of species, but with few specimens of each, although it is impossible to generalize because much depends upon the size of the estuary (e.g. Wagner 1957; Kilenyi 1969; Whatley and Kaye 1971). Another imponderable is the tidal range, which affects the amount of transportation from the sea, and is itself determined by the palaeogeography. The polyhaline fauna of bays and lagoons is more restricted in numbers of species, many of which have their main habitat in the lagoons, and in that sense can be regarded as being more specialized than estuarine faunas. The fauna of the Headon Beds appears more similar to a lagoonal fauna than an estuarine one. Estuaries may, of course, enter into lagoons before reaching the sea, and many coastlines are a complex mixture of bays, lagoons, and estuaries. The procedure adopted is to look for a model in the present world, the most suitable being the complex system of bays and lagoons developed along the Texan coast.

These have been more intensively studied than other similar coastlines. The Hampshire Basin in late Eocene times exhibited features similar to those of Texas. Ladd *et al.* (1957) considered that the best classification of the lagoons was based on salinity, giving closed bays ($0-20\text{‰}$) and polyhaline bays ($> 16.5\text{‰}$). The latter are 'front bays' directly connected with the Gulf of Mexico by openings between sandy barrier islands, while the closed bays have no direct connection. Coastal streams drain into the lagoons, and salinity changes are gradual between the various bays. Short-term fluctuations occur: due to periods of drought, giving higher salinities; periods of high rainfall and floods, giving lower salinities; and periods of hurricanes and storms, when the sea may be swept into the lagoons. These rapid changes lead to the mass mortality of many of the animals inhabiting the waters of the lagoons. The lagoons are very shallow, mostly less than 9 ft deep. Studies in Florida show similar features; at Cape Romano (Benda and Puri 1962) a barrier of mangrove islands separates lagoons from the open sea. The lagoons are about 4 ft deep, with a salinity of $13-43\text{‰}$; the mangrove swamps have numerous shallow baylets and inlets, with a salinity of $23-40\text{‰}$.

Ostracod assemblages from these areas have been studied by Swain (1955; San Antonio Bay, a closed lagoon, Texas); Curtis (1960; Mississippi Delta); Benda and Puri (1962; Cape Romano, Florida); Hulings and Puri (1964; Florida); Engel and Swain (1967; Texas Gulf coast).

Assemblages III and IV are characteristic of the typical Bay Facies of Swain and the 'closed shallow lagoon, away from fluvial influence and with little marine influence' of Curtis. For reasons already given, Assemblage III is believed to represent a lower mesohaline environment ($3-9\text{‰}$) and Assemblage IV higher mesohaline ($9.0-16.5\text{‰}$). These would then correspond to the Upper Bay and Mid Bay subfacies respectively of Swain. Assemblage V corresponds well with the Lower Bay subfacies of Swain and the 'open lagoon, small fluvial influence; marine influence prominent' of Curtis. This is the polyhaline facies of Ladd *et al.*, where the lagoon has a connection with the open sea.

The environment envisaged for these deposits, therefore, is a series of lagoons, some open, i.e. with a direct sea connection, others closed, i.e. no direct connection



TEXT-FIG. 8. Suggested environments of the ostracod assemblages.

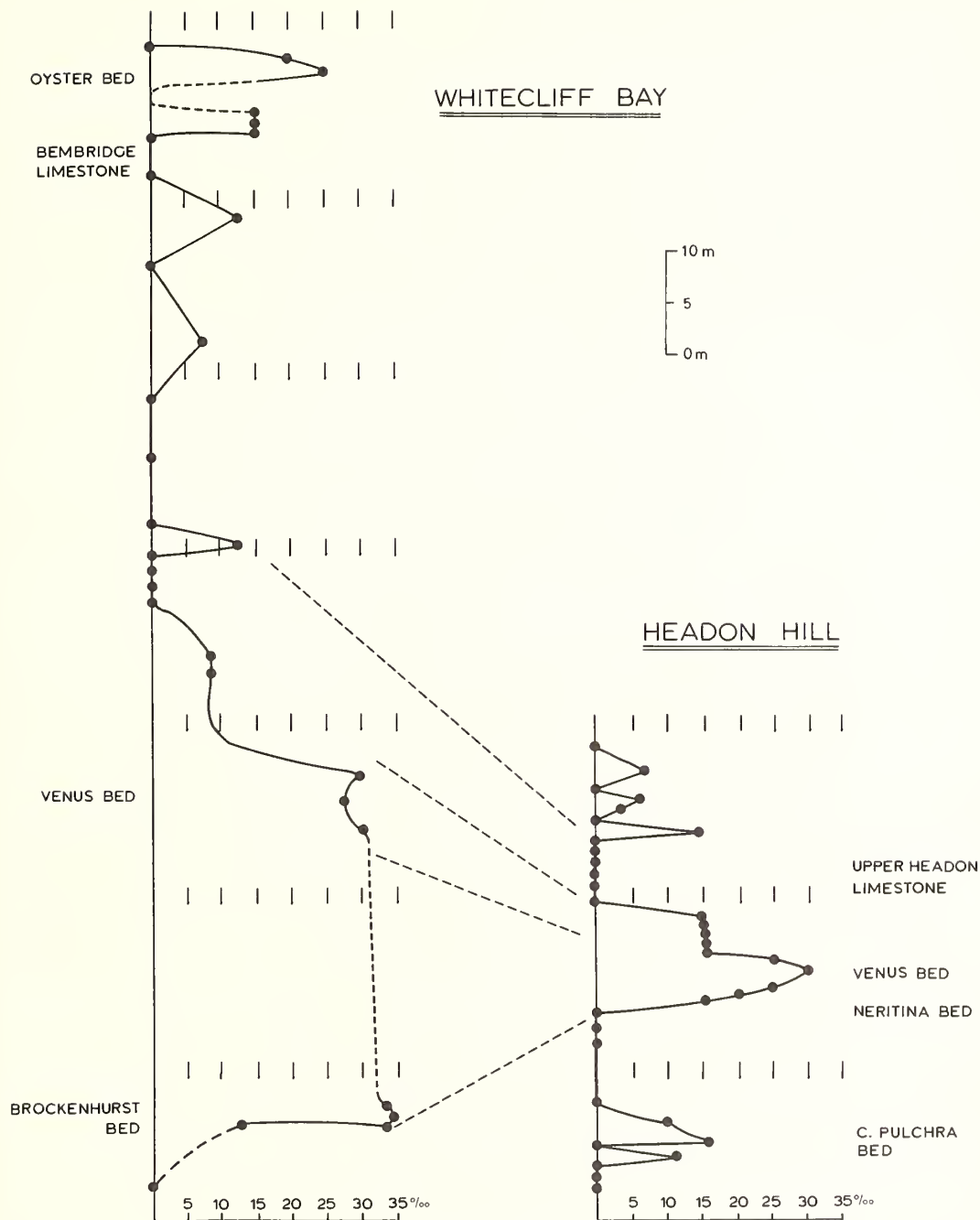
with the sea (text-fig. 8). In the polyhaline parts of the open lagoons there existed a fairly rich ostracod fauna, varying according to proximity to the sea. Oyster banks were also extensively developed. Further away from the sea connections, the water became progressively less saline, so that areas of Assemblages III and IV would be met. The fauna became poorer in number of species, but was very rich in individuals. In the mesohaline parts of the open lagoons it is probable that the 'banks' of *Batillaria ventricosa* would have been found, with the ostracod *Bradleya favosa*. Samples with worn molluscan shells and common *Haplocytheridea* and *Neocyprideis* might represent a channel connection between a closed and an open lagoon.

SALINITY PROFILES

Bearing in mind all the foregoing discussion, it is possible to allocate a salinity value to each sample. These have been plotted in text-fig. 9 to give salinity profiles for the major sections. Such profiles could be useful for correlation (see below).

DISTRIBUTION OF THE ASSEMBLAGES

The difficulty with such variable beds as these is that correlations tend to be based on facies rather than strict chronological units. For example, the Venus Beds of



TEXT-FIG. 9. Salinity profiles determined from ostracod assemblages.

Whitecliff Bay and Headon Hill are usually correlated; but in fact it is quite possible that the Venus Bed of Headon Hill is a time equivalent of the Brockenhurst Bed and Psammobia Bed. This would correlate the 'most marine' deposits of the eastern and western parts of the basin, and accepts that the marine influence becomes stronger eastwards. This is particularly apparent in the salinity profiles. At both ends of the island a fairly rapid increase in salinity is indicated, followed by a period of slightly lower salinity before returning to freshwater conditions. In the east the high salinity phase is 35‰, the lower 25‰, in the west 30‰ and 16‰. Curry (1965) has in fact suggested that the Venus Bed facies was deposited in lagoons around the Brockenhurst Sea, and Vella (1969) has correlated the Brockenhurst Bed with the Neritina Bed of Colwell Bay, and the Roydon Zone of Whitecliff Bay with the Venus Bed of Colwell Bay.

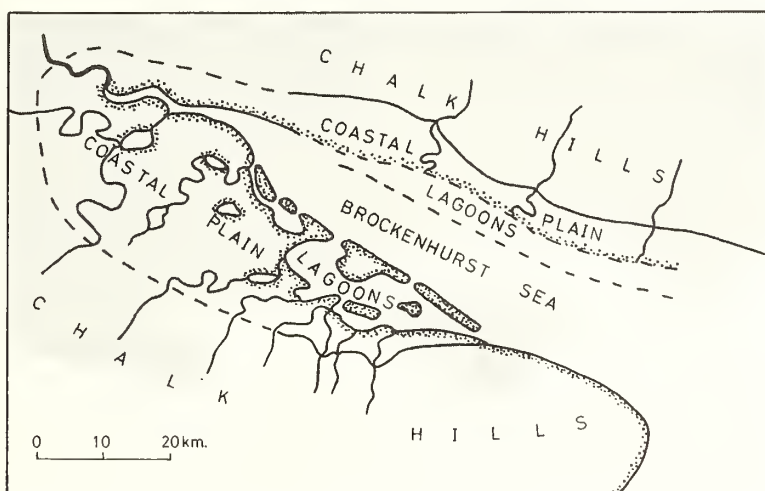
The distribution of Assemblage VI suggests that true marine conditions were only present at Whitecliff Bay and in the New Forest. Assemblage V on the other hand, is present at these localities and also at Colwell Bay, Milford, and Headon Hill. Mesohaline elements such as *Neocyprideis* are totally lacking in Assemblage V at Whitecliff Bay, while they are present at the other places, suggesting less marine influence in the west. This is also borne out by the Bembridge Oyster Bed, which contains a weakly developed Assemblage V at Whitecliff Bay, and Assemblages III and IV at Bouldnor Cliff. This bed is probably the nearest there is to a time plane throughout the whole sequence.

Assemblage IV is mainly present at the western end of the Isle of Wight. In the east it is only found in the Lower Headon Beds and the Bembridge Oyster Bed. Its principal development is in the upper part of the Middle Headon Beds and the Upper Headon Beds of Headon Hill, and it is possible that these are partly time equivalents of the development of Assemblage V in the east (i.e. the Venus Bed). Assemblage III has its main occurrence in the Upper Headon Beds and Osborne Beds of the east, but it is present in the Lower Headon Beds of the west. Once again, it is quite possible that the development of Assemblage III in the east occurred at the same time as that of Assemblages I and II in the west. Assemblage I is found in the Lower and Upper Headon Beds of the west and the Bembridge Limestone, while Assemblage II is found in the Lower Headon Beds of Paddy's Gap (Milford), and the Upper Headon Beds.

COMPARISON WITH FORAMINIFERAL STUDIES

The most detailed works published to date are those of Bhatia (1957) and Murray and Wright (1974) concerning the foraminiferal faunas. Bhatia regarded the fauna of the Brockenhurst Beds as indicating deeper-water infraneritic conditions shallowing in the Psammobia Beds. The Venus Bed was taken to indicate shallow epineritic becoming lagoonal and less saline. Murray and Wright have indicated that more modern data favours depths shallower than these. They took the foraminiferids of the Brockenhurst Beds, dominated by *Quinqueloculina*, *Triloculina*, and *Cibicides*, to indicate the seaward part of an enclosed lagoon with normal or slightly hyper-saline salinities; planktonic foraminiferids present in these beds were thought to have been transported into the lagoon from the open sea. The Venus Bed has a low

diversity of foraminiferids, and at Whitecliff Bay the succession was interpreted as showing the inner part of a hyposaline lagoon, giving way to a normal marine lagoon. At Headon Hill the foraminiferids are small, usually juveniles, so an abnormal environment was postulated, with intertidal lagoons, salinity $> 32\text{‰}$ and hyposaline subtidal lagoons or estuaries. The limestones of the Upper Headon Beds at Headon Hill yielded foraminiferids at three horizons which were taken to indicate a lagoonal environment with salinity $> 32\text{‰}$. The dominant genera are *Rosalina* and *Quinqueloculina*. The former was also found near the top of the lowermost limestone of the Bembridge Limestone at Whitecliff Bay, and interpreted as indicating very unfavourable conditions with a salinity $< 10\text{‰}$. The lowest part of the Bembridge Marls at Whitecliff Bay were interpreted as hyposaline lagoonal deposits, or an estuary, salinity $10\text{--}25\text{‰}$.



TEXT-FIG. 10. The palaeogeography of the Hampshire Basin during the time of the deposition of the Brockenhurst Beds. This is intended to show the relationship between the main geographical units, and is not an exact geography. The boundaries between the coastal plain, lagoons, and sea fluctuated considerably, so that the positions of the individual lagoons and their outlets are conjectural. Evidence has been used from many sources, both consciously and subconsciously, incorporating stratigraphy, structure, sedimentation, and palaeontology. In particular, it owes much to the work of Dr. N. Edwards, although of course he may not entirely agree with the end result, and the responsibility is mine.

There seems to be close agreement between these results and those of the present study. There is a difference in interpretation of the Brockenhurst Beds, but this may be semantic because their text-fig. 28 indicates a similar interpretation to text-fig. 10 of this study. Within the hyposaline environment the ostracods offer more scope for finer detail than the Foraminifera, so that rather more environmental assemblages can be recognized. A second point of apparent disagreement is with the Upper Headon limestones of Headon Hill; Murray and Wright indicate polyhaline or

marine salinities, while this study indicates predominantly freshwater conditions. However, it has to be borne in mind that thin beds exist within the limestones that have yielded mesohaline ostracods (see text-fig. 1), while the main mass of limestone, with its abundant freshwater molluscan fauna, has not yielded any Foraminifera.

TAXONOMY

A study such as this inevitably leads to the discovery of new species. These are described in the following section. The faunal list given by Keen (1968) can now be revised as follows:

1968 name	Present name
<i>Candona</i> sp. A	<i>Candona cliffendensis</i> sp. nov.
<i>Candona</i> sp. B	<i>Candona daleyi</i> sp. nov.
<i>Cypridopsis</i> sp. A	<i>Cypridopsis hessani hantonensis</i> subsp. nov.
' <i>Eucypris</i> ' sp. A	<i>Virgatocypris edwardsi</i> sp. nov.
<i>Neocyprideis</i> cf. <i>williamsoniana</i>	<i>Neocyprideis colwellensis</i> (Jones)
<i>Brachycythere</i> sp. A	<i>Ruggieria semireticulata</i> Haskins
<i>Cushmanidea</i> sp. A	<i>Cushmanidea haskinsi</i> sp. nov.
<i>Cushmanidea</i> sp. B	<i>Cushmanidea wightensis</i> sp. nov.
<i>Haplocytheridea</i> sp. A	<i>Haplocytheridea mantelli</i> Keen
<i>Limnocythere</i> sp. A	<i>Cladarocythere hantonensis</i> Keen
<i>Paracytheridea</i> sp. A	<i>Paracytheridea gradata</i> (Bosquet)
<i>Schuleridea</i> sp. A	<i>Schuleridea perforata headonensis</i> subsp. nov.

SYSTEMATIC DESCRIPTIONS

The classification is that of the *Treatise* (Moore 1961). In the descriptions, the heading 'Material' refers to the total sample examined; the numbers refer to individual specimens deposited at the British Museum (Natural History), prefixed Io.

Abbreviations. L = length, H = height, W = width; measurements are in millimetres.

Order PODOCOPIDA Muller, 1894
 Suborder PODOCOPINA Sars, 1866
 Superfamily CYPRIDACEA Baird, 1845
 Family CYPRIDIDAE Baird, 1845
 Genus CYPRIDOPSIS Brady, 1868
Cypridopsis hessani Carbonnel and Ritzkowski, 1969
Cypridopsis hessani hantonensis subsp. nov.

Plate 46, figs. 9-11

1975 *Cypridopsis* sp. A, Keen, p. 275.

Derivation of name. After Hampshire.

Type locality. Upper Headon Beds, Headon Hill (HH53).

Distribution. Sample HH53 only.

Holotype. Io 6736, female left valve.

Material. Over 100 valves. Registered specimens Io 6736-6739.

Dimensions. Holotype, female left valve, Io 6736: L, 0.44; H, 0.25; L/H, 1.76; W/2, 0.11. Female right valve, Io 6737: L, 0.43; H, 0.24. Male left valve, Io 6738: L, 0.44; H, 0.23; L/H, 1.91; W/2, 0.10. Male right valve, Io 6739: L, 0.44; H, 0.23.

Diagnosis. Small, elongate, small denticles along anterior margin of right valve.

Description and discussion. The nominate subspecies was described from the Melanienton (Rupelian) of Hesse, Germany; it differs from the present subspecies by its large size (0.53 cf. 0.44) and in details of lateral outline. Carbonnel and Ritzkowski were unable to recognize sexual dimorphism; the L/H ratio given by them, 1.88, is closer to that of the male in the Headon samples, but as there are differences in lateral outline, and because it is virtually unknown to have a sample consisting of males only, it is advisable to compare the nominate subspecies with both sexes. The female left valve of *C. hessani hantonensis* differs in having a well-defined highest point with an evenly curved antero-dorsal margin; the male left valve has a more evenly curved dorsal margin, lacking the cardinal angles of *C. hessani hessani*. Sexual dimorphism is not as prominent in the right valve; the ventral margin is more concave than in *C. h. hessani*.

Internal details as for the genus; the central muscle scars cannot be clearly seen, but appear to be typical of *Cypridopsis*; large anterior vestibule present, with numerous short radial pore canals.

Genus VIRGATOCYPRIS Malz and Moayedpour, 1973

Virgatoocypris edwardsi sp. nov.

Plate 47, figs. 3, 6, 9, 12

1968b ?*Scottia* sp. Haskins, p. 5, pl. 1, figs. 7-9.

1975 *Eucypris* cf. *tenuistriata* (Dollfus); Keen, p. 272.

Derivation of name. In honour of Dr. N. Edwards.

Type locality. Lower Headon Beds, Headon Hill (HH23).

Distribution. Lower and Upper Headon Beds of Headon Hill and Colwell Bay.

Holotype. Io 6740, a left valve.

Material. Eight complete adult valves, several fragments, forty-five larval stages. Registered specimens Io 6740-6743.

Dimensions. Holotype, left valve, Io 6740: L, 1.13; H, 0.65; L/H, 1.72. Right valve, Io 6741: L, 1.16; H, 0.66; L/H, 1.76.

Diagnosis. Dorsal margin with prominent, pointed, highest point; ventral margin convex.

Description. See Plate 47, figs. 3, 9 for lateral outline. The valves are swollen ventrally. The surface of the valve has fine longitudinal striations; no unornamented specimens have been observed. Internally features are as for the genus: a conspicuous selvage, large anterior vestibule, numerous straight radial pore canals; the central muscle scars have not been clearly observed.

Discussion. This differs from other species principally in lateral outline. *V. tenuistriata* (Dollfus) (Oligocene, Paris Basin) is more elongate and ovoid; *V. straubi* (Carbannel and Ritzkowski) (Oligocene, Hesse) has its highest point nearer anterior and has a pronounced concave ventral margin in the right valve; *V. virgata* Malz and Moayedpour (Miocene, Germany) is more elongate, has a straighter dorsal margin, and a straight ventral margin; *V. grisysensis* (Margerie) (Upper Eocene, Paris Basin) is smaller, has a weakly developed selvage, and has its highest point placed medianly giving a symmetrically curved dorsal margin. The exact pattern of striations also appears to differ amongst these species.

The specimens of *Virgatocypris* from the Bembridge Limestone have been left in open nomenclature. They differ from the Headon forms in being slightly more elongate, having a less-pointed dorsal margin, and a slightly more tapered posterior. Jones and Sherborn (1889, p. 43) described a new species from the Bembridge Limestone of West Cowes, *Pseudocythere bristovi*, which might be a species of *Virgatocypris*. Two specimens of this species are preserved in the collections of the Institute of Geological Sciences, Mik (T) 712 001 and 712 002, neither being type material. The specimens are incomplete, in limestone, and their identity difficult to determine; they are not the same as the Headon species, however.

Family CANDONIDAE Kaufmann, 1900

Genus CANDONA Baird, 1845

Candona cliffendensis sp. nov.

Plate 46, figs. 6-8

†1889 *Pontocypris* (?) sp. Jones and Sherborn, p. 16, pl. 1, fig. 13a.

1968b ?*Candonopsis* sp. Haskins, p. 7, pl. 2, figs. 23-27.

1975 *Candona* (*Pseudocandona*) sp. B. Keen, p. 272.

Derivation of name. After the type locality.

Type locality. Upper Headon Beds, Cliff End (Colwell Bay, CB12).

Distribution. Lower and Upper Headon Beds of Headon Hill and Colwell Bay; Osborne and Bembridge Beds of Whitecliff Bay.

Holotype. Io 6744, a left valve.

EXPLANATION OF PLATE 46

Figs. 1-5. *Candona daleyi* sp. nov. 1, 2, holotype, Io 6747, Lower Headon Beds of Headon Hill. 1, right valve internal view, $\times 70$. 2, central muscle scars, $\times 450$. 3-5, Upper Headon Beds of Colwell Bay (CB12), $\times 70$. 3, left valve of moult no. 7, Io 6749. 4, right valve of moult no. 7, Io 6750. 5, left valve of moult no. 8, Io 6748.

Figs. 6-8. *Candona cliffendensis* sp. nov. 6, Upper Headon Beds of Headon Hill (HH53), left valve of moult no. 7, Io 6746, $\times 70$. 7, 8, Upper Headon Beds of Colwell Bay (CB12). 7, right valve internal view, specimen destroyed, $\times 70$. 8, stereo-pair, right valve of holotype, $\times 50$.

Figs. 9-11. *Cypridopsis hessani hantonensis* subsp. nov., Upper Headon Beds of Headon Hill (HH53), $\times 140$. 9, holotype, female left valve, Io 6736. 10, male left valve, internal view, Io 6738. 11, female right valve, Io 6737.

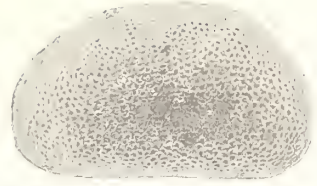
Fig. 12. *Cypria dorsalis* Malz and Moayedpour, left valve, internal view, Io 6734, Lower Headon Beds of Headon Hill (HH30), $\times 125$ (L = 0.54 mm).



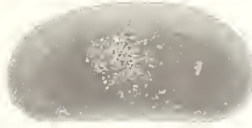
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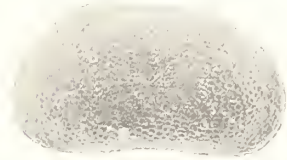
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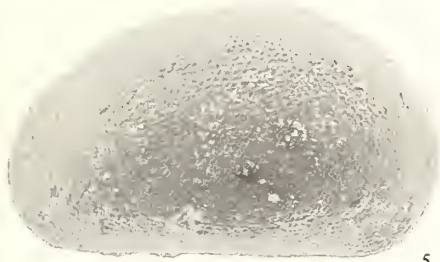
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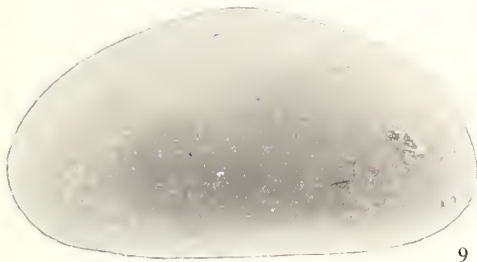
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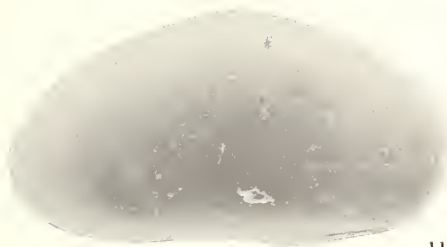
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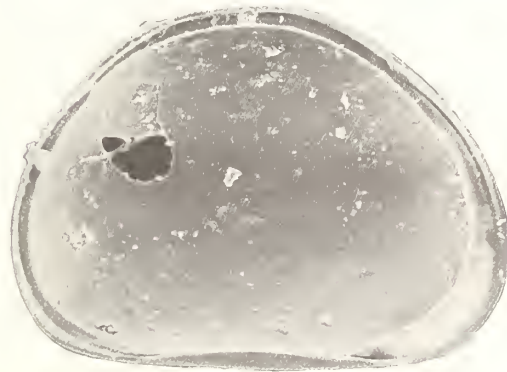
9



10



11



12

Material. Six adult valves, forty larval stages. Registered specimens Io 6744–6746.

Dimensions. Holotype, right valve, Io 6744: L, 0.84; H, 0.41; L/H, 2.05; left valve, Io 6745: L, 0.85; H, 0.42; L/H, 2.02. Larval 8, right valve, Io 6746: L, 0.68; H, 0.34; L/H, 2.00. Larval 7, right valve, Io 6746: L, 0.50; H, 0.24; L/H, 2.05.

Diagnosis and description. For lateral outline see Plate 46, figs. 7–9. L/H 2.00; larval stages smooth. Internal details as for the genus.

Discussion. This is distinguished from other Tertiary species by its elongate shape and smooth larval stages (see *C. daley* below for discussion). The anterior and posterior cardinal angles suggest it belongs to *Candona* rather than *Candonopsis* Vavra, although the elongate shape is more characteristic of the latter.

Candona daley sp. nov.

Plate 46, figs. 1–5

1968b *Potamocypris* sp. Haskins, p. 6, pl. 1, figs. 17–22.

1975 *Candona* (*Pseudocandona*) sp. A, Keen, p. 272.

Derivation of name. In honour of Dr. B. F. Daley.

Type locality. Lower Headon Beds, Headon Hill (HH23).

Distribution. Lower and Upper Headon Beds and Osborne Beds of Headon Hill, Colwell Bay, Whitecliff Bay; Middle Headon Beds of Headon Hill; Bembridge Limestone of Whitecliff Bay and Bouldnor Cliff.

Holotype. Io 6747, a right valve.

Material. Two adult right valves, numerous larval stages. Registered specimens Io 6747–6750.

Dimensions. Holotype, right valve, Io 6747: L, 0.87; H, 0.55; L/H, 1.58. Larval 8, left valve, Io 6748: L, 0.81; H, 0.52. Larval 8, right valve: L, 0.75; H, 0.46. Larval 7, left valve: Io 4749: L, 0.58; H, 0.36. Larval 7, right valve: Io 4750: L, 0.53; H, 0.33.

Diagnosis. Highest point near posterior; distinct antero-dorsal notch seen in lateral view; L/H 1.58; larval stages punctate.

EXPLANATION OF PLATE 47

Figs. 1, 2. *Cushmanidea stintoni* sp. nov., $\times 120$, Middle Headon Beds of Headon Hill. 1, left valve of female, holotype, Io 6766. 2, right valve of female, Io 6767.

Figs. 3, 6, 9, 12. *Virgatocypris edwardsi* sp. nov. 3, 6, holotype, Io 6740, Lower Headon Beds of Headon Hill. 3, stereo-pair, left valve, $\times 48$. 6, stereo-pair, enlargement showing simple normal pore canals with rims, $\times 300$. 9, 12, Upper Headon Beds of Colwell Bay (CB12). 9, right valve, Io 6741, $\times 48$. 12, internal view of right valve, Io 6742, $\times 55$.

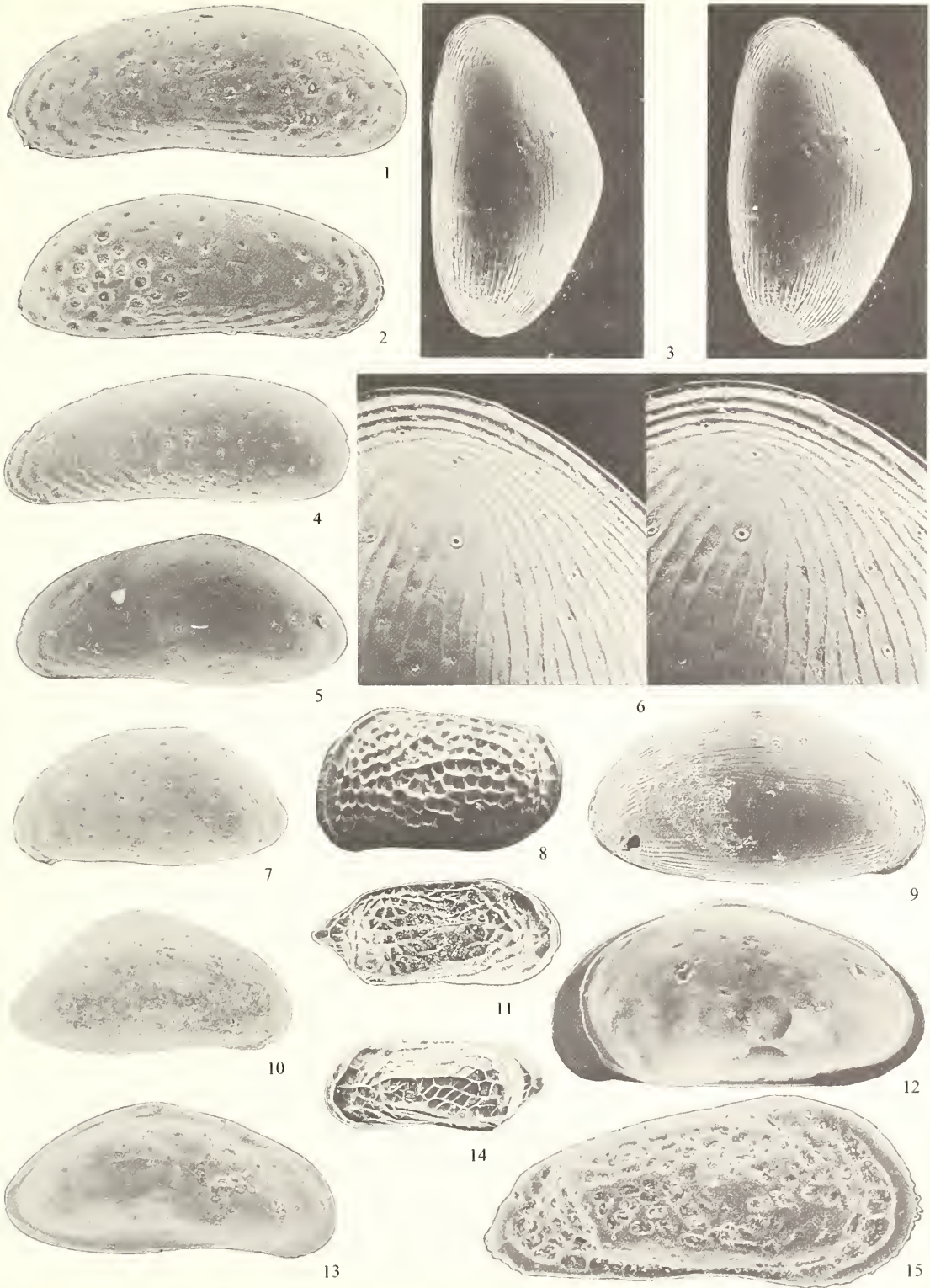
Fig. 4. *Cushmanidea haskinsi* sp. nov., $\times 84$, left valve of female, holotype, Io 6761, Middle Headon Beds of Headon Hill.

Figs. 5, 7, 10, 13. *Cushmanidea wightensis* sp. nov., $\times 70$, Middle Headon Beds of Headon Hill. 5, left valve of male, Io 6773. 7, left valve of female, holotype, Io 6771. 10, right valve of female, Io 6772. 13, internal view of male left valve, Io 6774.

Fig. 8. *Loxoconcha* sp., L = 0.48, left valve, Io 6783, Middle Headon Beds of Headon Hill.

Figs. 11, 14. *Cytherura pulchra* sp. nov., $\times 100$, Lower Headon Beds of Headon Hill. 11, right valve, Io 6777. 14, left valve, holotype, Io 6776.

Fig. 15. *Idiocythere bartoniana* Haskins, L = 0.47, right valve, Io 6781, Brockenhurst Beds of Whitecliff Bay.



KEEN, Upper Eocene ostracods

Description. For lateral outline see Plate 46, fig. 1. Adult right valve has a prominent rim around the anterior, ventral, and posterior margins. Surface is smooth in adult, punctate in larval stages. Internal details as for the genus. The right valve of the penultimate larval stage has a similar outline to the adult, including the antero-dorsal notch; the left valve of the penultimate larval stage may therefore indicate the outline of the left valve of the adult.

Discussion. According to Triebel (1963) this species should be placed in the sub-genus *Candona* (*Pseudocandona*) Kaufmann, 1900, on account of the punctate larval stages. However, recent opinion (especially Dr. R. Meyrick, pers. comm. 1974) would only separate these on soft-part morphology. Thus, no subgeneric status is designated. *C. daleyi* differs from *C. fertilis* Triebel in lateral outline, especially the presence of the antero-dorsal notch, and in the presence of a marginal rim.

The larval stages of this species are very common in freshwater sediments of the Headon-Bembridge series; they are distinguished from larval *C. cliffendensis* by being shorter and punctate, and from the undescribed species from the Hamstead Beds (Keen 1972a, p. 283, pl. 47, fig. 8) by being shorter.

Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925
Subfamily CYTHERIDEINAE Sars, 1925
Genus NEOCYPRIDEIS Apostolescu, 1956
Neocyprideis colwellensis (Jones)

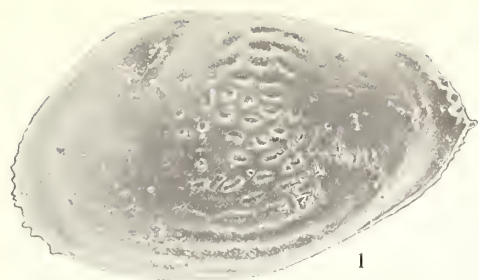
Plate 48, figs. 5-12

- 1857 *Cytherideis colwellensis* Jones (pars), p. 49, pl. 14, fig. 13.
1889 *Cytherideis colwellensis* Jones; Jones and Sherborn (pars), p. 45.
1960 *Neocyprideis* aff. *williamsoniana* (Bosquet); Kollmann, p. 177, pl. 3, fig. 2a-b; pl. 12, fig. 8; pl. 20, figs. 8-10.
1969 *Cyprideis* (*Neocyprideis*) *williamsoniana* (Bosquet); Haskins, p. 155, pl. 4, figs. 10-20.

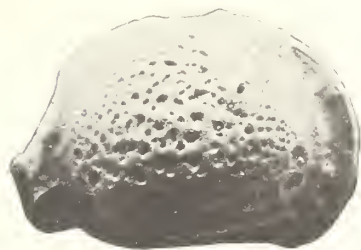
Type locality and distribution. Colwell Bay; Headon-Osborne Beds.

EXPLANATION OF PLATE 48

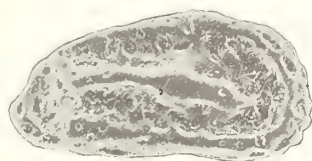
- Fig. 1. *Ruggieria semireticulata* Haskins, L = 0.88, left valve, Io 6780, Middle Headon Beds of Whitecliff Bay (WB22).
Fig. 2. *Pokornyella osnabrugensis* (Lienenklaus), L = 0.59, right valve, Io 6782, Middle Headon Beds of Headon Hill (HH43).
Figs. 3, 4. *Hazelina indigena* Moos, Brockenhurst Beds of Whitecliff Bay. 3, right valve of female, Io 6778, L = 0.54. 4, right valve of male, Io 6779, L = 0.57.
Figs. 5-12. *Neocyprideis colwellensis* (Jones), all specimens from Headon Hill, figs. 5, 11 from Upper Headon Beds (HH58), remainder from Middle Headon Beds (HH48). 5, left valve of male of a smooth form, Io 6753, $\times 55$. 6, stereo-pair, right valve of female punctate form, Io 6751, $\times 55$. 7, stereo-pair, right valve of male punctate form, Io 6752, $\times 55$. 8, stereo-pair, left valve of moult no. 8 showing development of nodes, note that each 'node' is in fact a cluster of small nodes, Io 6755, $\times 75$. 9, detail of anterior part of hinge of Io 6754 (see also fig. 10), $\times 350$. 10, internal view of female right valve, Io 6754, $\times 55$. 11, sieve type normal pore canal of Io 6753 (see also fig. 5), $\times 1300$. 12, central muscle scars of Io 6754 (see also fig. 10), $\times 300$.



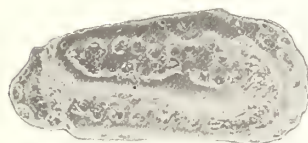
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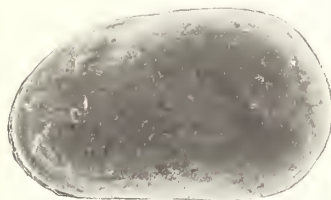
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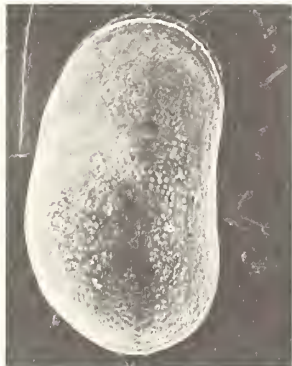
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6



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8



11



12

Lectotype. BM(NH), I 6431 (13). Jones figured two species under the name *Cytherideis colwellensis*; one has subsequently been described as *Cytheretta rhenana headonensis* Haskins, 1968. Keen (1972a) and Malz (1973) independently chose the remaining specimen as the lectotype of *Neocyprideis colwellensis*. The specimen is a larval stage, but adult topotype material is abundant.

Material. Registered specimens Io 6751–6755.

Diagnosis. Has similar-sized valves, males and females have similar L/H ratios, female carapace inflated at posterior end; anterior and median hinge elements of equal length; twenty anterior radial pore canals; surface with dorsal sulcus.

Discussion. There are nine described species of *Neocyprideis* ranging from the upper Cretaceous to the Miocene. Many of these form part of a continuous phyletic lineage, which makes specific determination difficult unless there is sufficient material for population studies. The two species most closely resembling *N. colwellensis* are *N. apostolescui* (Keij), thought to be its ancestor, and *N. williamsoniana* (Bosquet), which is probably its descendant. Specimens from the Bembridge Beds have been placed in the latter. *N. apostolescui* differs in having a more evenly rounded anterior end when seen in lateral view, has a more curved anterior hinge element which is shorter than the median element, and has fewer anterior radial pore canals (16–19 cf. 17–24). Keij (1957) used the absence of a punctate surface to differentiate *N. apostolescui* from *N. williamsoniana*; as indicated earlier, this character is probably phenotypic, and all species of *Neocyprideis* may be smooth or punctate. *N. williamsoniana* differs from *N. colwellensis* in having more clearly differentiated sexes using L/H measurements, a more angular postero-dorsal angle, especially when viewed from the inside of the valve, a weaker dorsal sulcus, and the posterior inflation of the female carapace is situated in a more dorsal position.

Noding. *N. colwellensis* has ten node positions (text-fig. 11), although several of these are frequently joined by the development of smaller nodes between them. A node may be a single tubercle, or a cluster of small tubercles (Pl. 48, fig. 8). All nodes are present in the adult and instars 7 and 8, but earlier instars have fewer nodes, although there does not seem to be any orderly appearance of nodes during ontogeny. Nodes are present on both valves and both sexes with equal frequency.

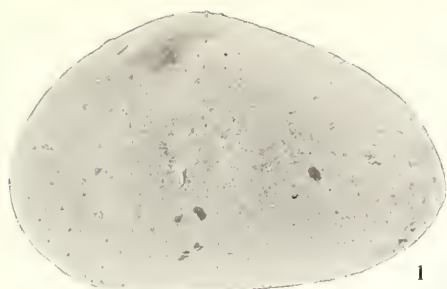
EXPLANATION OF PLATE 49

Figs. 1–4. *Schuleridea (Aequacytheridea) perforata headonensis* subsp. nov., $\times 70$, Middle Headon Oyster Bed of Colwell Bay. 1, left valve of female, holotype, Io 6756. 2, right valve of female, Io 6757. 3, left valve of male, Io 6759. 4, internal view of left valve of female, Io 6758.

Figs. 5, 6. *Eocytheropteron wetherelli* (Jones), L = 0.70, Middle Headon Beds of Headon Hill (HH43), stereo-pairs. 5, female right valve. 6, normal pore canal showing a larger central pore within the sieve-type pore canal, $\times 1500$.

Figs. 7, 8. *Leguminocythereis delirata* (Jones and Sherborn), L = 0.82, Middle Headon Beds of Headon Hill (HH43). 7, normal pore canals showing a larger central pore within the sieve-type pore canal, $\times 400$. 8, female left valve.

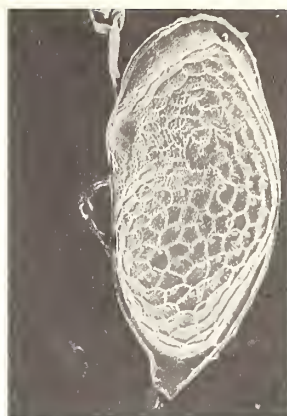
Figs. 9, 10. *Cytheromorpha bulla* Haskins, L = 0.64, Lower Headon Beds of Headon Hill (HH26). 9, female left valve. 10, stereo-pair showing sieve-type normal pore canals, $\times 170$.



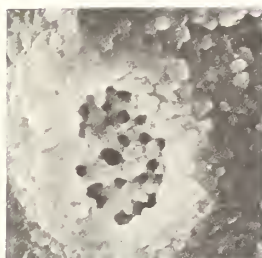
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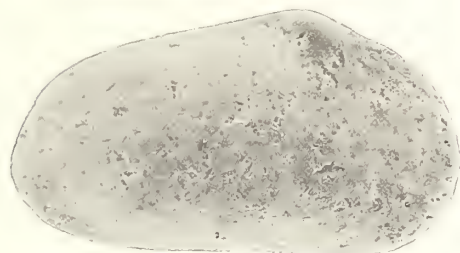
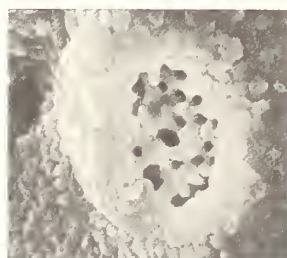
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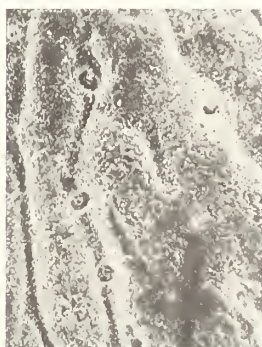
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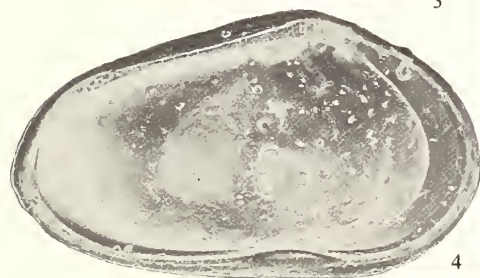
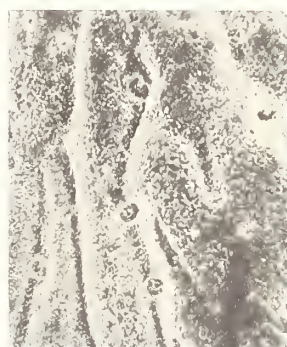
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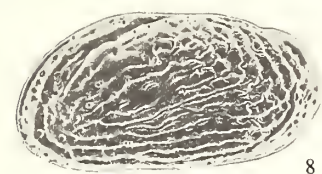
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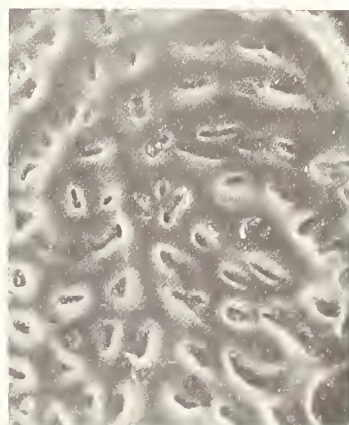
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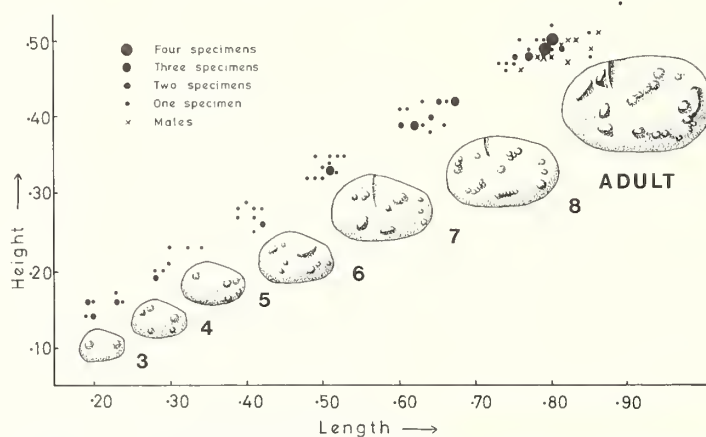


9



9

Larval stages. Six juvenile stages have been recognized; text-fig. 11 shows the changes in lateral outline during ontogeny; note the triangular outline with highest point at anterior in the early stages. A punctate surface has been observed in instars 7 and 8, but earlier instars are smooth. The hinge elements are crenulate for instars 6, 7, and 8 and appear to be so for earlier instars. The median element occupies more than 50% of the hinge length in instars 3–7, with a reduced anterior element; the latter increases for instar 8 and is equal to the median element in the adult. The posterior hinge element retains a similar proportion throughout ontogeny. The number of radial pore canals increases during ontogeny from an average of six in instar 4 to twenty in the adult. These changes during ontogeny parallel the changes seen in phylogeny.



TEXT-FIG. 11. Size distribution of *Neocyprideis colwellensis* (Jones) from the Cyrena pulchra Bed (Lower Headon Beds) of Headon Hill (HHCP2).

Genus SCHULERIDEA Swartz and Swain, 1946

Subgenus SCHULERIDEA (AEQUACYTHERIDEA) Mandlestam, 1947

Schuleridea (Aequacytheridea) perforata (Roemer)

Schuleridea (Aequacytheridea) perforata headonensis subsp. nov.

Plate 49, figs. 1–4

1857 *Cytheridea perforata* Roemer; Jones, p. 44 (pars), pl. IV, fig. 14a–e.

1889 *Cytheridea perforata* Roemer; Jones and Sherborn, p. 39 (pars).

1969 *Schuleridea perforata* (Roemer); Haskins, p. 161 (pars).

Derivation of name. After the Headon Beds.

Type locality. Colwell Bay (Oyster Bed).

Distribution. Venus Bed of Headon Hill, Colwell Bay, and Whitecliff Bay.

Holotype. Io 6756, a female left valve.

Material. Forty-seven valves. Registered specimens Io 6756–6760.

Dimensions. Mean of eleven female left valves: L, 0.82; H, 0.53; L/H, 1.56. Mean of three male left valves: L, 0.89; H, 0.52; L/H, 1.70.

Diagnosis. Pronounced sexual dimorphism, elongate carapace, prominent posterior cardinal angle, no marginal spines or denticles, surface finely punctate.

Discussion. According to the literature *S. (A.) perforata* is one of the most widely ranging species of ostracods in a stratigraphical sense; it is found from the Palaeocene to Miocene. Moos (1970) and Malz (1973) have shown how it is possible to recognize distinct species and subspecies by careful study of the lateral outline and ornamentation. Internal features do not vary greatly, and the new subspecies is very similar to the nominate subspecies in this respect. *S. (A.) perforata headonensis* differs in being more elongate and showing more distinct sexual dimorphism: L/H female 1.56 cf. 1.47 (*S. (A.) perforata perforata* from Damery), male 1.70 cf. 1.57. The dorsal margin has a more pronounced posterior cardinal angle; the nominate subspecies almost lacks this, and so has a more tapered and triangular appearance. The posterior margin of the nominate subspecies is pointed, which in *S. (A.) perforata headonensis* it is not. The ventral margin is straight to convex, while the nominate subspecies is straight to concave. The surface is punctate, but this ornamentation does not often show very clearly because of the mode of preservation.

Subfamily NEOCYTHERIDEIDINAE Puri, 1957

Genus CUSHMANIDEA Blake, 1933

Cushmanidea haskinsi sp. nov.

Plate 47, fig. 4

- 1857 *Cytherideis flavida* Jones (non Muller), p. 50 (pars).
- 1889 *Cytherideis* sp. Jones and Sherborn, p. 45.
- ?1970 *Cushmanidea grosjeani* Haskins (non Keij), p. 16 (pars), pl. 1, figs. 16, 18, 19, 21.
- ?1970 *Cushmanidea* sp. Haskins, p. 16, pl. 1, figs. 22-23.

Derivation of name. In honour of Dr. C. W. Haskins.

Type locality. Middle Headon Beds (Venus Bed), Headon Hill.

Distribution. Venus Bed of Headon Hill, Oyster Bed of Colwell Bay, and ?Middle Headon Beds of Whitecliff Bay.

Holotype. Io 6761, a female left valve.

Material. Seventeen valves and carapaces. Registered specimens Io 6761-6765.

Dimensions. Female carapace, Io 6764: L, 0.62; H, 0.27; W, 0.25; L/H, 2.30. Male carapace, Io 6765: L, 0.72; H, 0.28; W, 0.26; L/H, 2.57.

Diagnosis. Elongate, eight to nine faint ridges parallel to anterior margin, large anterior and narrow posterior vestibules, radial pore canals simple.

Description. For outline and ornamentation see figured specimen. Note the eight to nine weak ridges developed in the anterior and antero-ventral areas, and running parallel to the anterior margin. There are some sixty normal pore canals which widen near the outer surface and appear to be of the sieve-type.

Internally, all the hinge elements are smooth; the duplicature has large anterior and narrow posterior vestibules, with 26 anterior, 16 ventral, and 7 posterior radial pore canals; the selvage is parallel to the outer margin. The central muscle scars consist of a row of 4 scars, the dorsal-most of which is usually indistinct; the frontal scar is irregular, but tendency towards a V shape; there are 2 small mandibular scars, and some 7 dorsal muscle scars.

Discussion. *C. lithodomoides* (Bosquet) has a similar ornamentation, differing by its stronger development and the ridges running parallel to the outer margin so that they are parallel to the ventral margin in their ventral portion. The closest species is *C. therwilensis* (Oertli) from the upper Oligocene of Switzerland; the ornamentation and internal features are very similar. The main difference is in lateral outline; the highest point is much nearer the posterior in *C. therwilensis*, and the posterior margin is more pointed. The material described by Haskins probably belongs here although his specimens are larger. The forms referred to as *C. grosjeani* are probably females, and *Cushmanidea* sp. the males.

Cushmanidea stintoni sp. nov.

Plate 47, figs. 1, 2

1970 *Cushmanidea grosjeani* Haskins (non Keij), (pars), p. 16, pl. 1, figs. 17, 20.

Derivation of name. In honour of Mr. F. C. Stinton, a worker on Tertiary otoliths and guide to the Tertiary of Hampshire.

Type locality. Middle Headon Beds (Venus Bed), Headon Hill.

Distribution. Venus Bed of Headon Hill, Middle Headon Beds and Bembridge Marls Oyster Bed of Whitecliff Bay.

Holotype. Io 6766, a female left valve.

Material. Twenty-four valves and carapaces. Registered specimens Io 6766-6770.

Dimensions. Female carapace, Headon Hill, Io 6768: L, 0.53; H, 0.23; W, 0.21; L/H, 2.30. Female carapace, Whitecliff Bay, Io 6769: L, 0.65; H, 0.27; W, 0.23; L/H, 2.33. Male carapace, Whitecliff Bay, Io 6770: L, 0.69; H, 0.26; W, 0.26; L/H, 2.62.

Diagnosis. Small, prominent pits at posterior, medium-sized anterior vestibule, simple radial pore canals.

Description. For lateral outline and ornamentation see figured specimens. Each of the pits seen on the surface of the carapace has a sieve-type normal pore canal opening into it. Viewed with an optical microscope, the pits are seen as being predominantly at the posterior, with a lesser development along the venter and anterior.

Internally, all hinge elements are smooth, the anterior and median elements of about equal length. The anterior vestibule is of medium size, ventral and posterior vestibules small. There are 35 anterior, 16 ventral, and 10 posterior simple radial pore canals; the selvage is parallel to outer margin. Central muscle scars a row of 4, dorsal-most is large; a single V-shaped frontal scar; 2 small mandibular scars.

Sexual dimorphism is apparent in the specimens from Whitecliff Bay, but not in those from Headon Hill; all the latter are presumed to be females. The Whitecliff Bay specimens are also larger, but otherwise identical.

Discussion. The most similar species is *C. neauphlensis* (Apostolescu) from the Lutetian of the Paris Basin. This differs in lateral outline, with its highest point slightly to the anterior of the mid-point, has strong pitting over the entire surface, and a median dorsal sulcus. Keij (1957) placed *C. neauphlensis* in the synonymy of *C. mayeri* (Howe and Garrett) from the Eocene of the U.S.A.; certainly the two species are very similar.

Cushmanidea wightensis sp. nov.

Plate 47, figs. 5, 7, 10, 13

Derivation of name. From the Isle of Wight.

Type locality. Middle Headon Beds (Venus Bed), Headon Hill.

Distribution. Venus Bed of Headon Hill, Oyster Bed of Colwell Bay.

Holotype. Io 6771, a female left valve.

Material. Twenty-two valves. Registered specimens Io 6771–6775.

Dimensions. Female carapace, Io 6775: L, 0.64; H, 0.33; W, 0.29; L/H, 1.94. Male left valve, Io 6773: L, 0.77; H, 0.34; L/H, 2.26.

Diagnosis. Not particularly elongate, unornamented, hinge elements crenulate, no vestibules, simple radial pore canals.

Description. For lateral outline seen figured specimens. Sexual dimorphism is very pronounced, although males are rare (3 out of 22 specimens). Right valve more pointed dorsally. There are 55–60 normal pore canals.

Internally, the hinge is crenulate; the anterior element has some 5 coarse denticles, median element very finely crenulate, posterior element coarse, with 6–7 denticles. Ratio of hinge-element lengths, anterior:median:posterior, 3:3:2. There are no vestibules; 16 anterior, 6 ventral, and 4 posterior simple radial pore canals; there is a suggestion in one specimen of a series of blind ventral radial pore canals. Central muscle scars consist of a vertical row of 4, all in contact, with 2 frontal scars very close together and often appearing as a single V-shaped scar. There is a prominent fulcral point, and 2 large mandibular scars.

Discussion. There are no other species with which to compare, and it is doubtful whether this is a true *Cushmanidea* species, because of the lack of vestibules and crenulate hinge.

Family CYTHERURIDAE G. W. Muller, 1894

Genus CYTHERURA Sars, 1866

Cytherura pulchra sp. nov.

Plate 47, figs. 11, 14

Derivation of name. After the Cyrena pulchra Bed.

Type locality. The Cyrena pulchra Bed, Headon Hill.

Distribution. Only recorded in the type deposit of Headon Hill.

Holotype. Io 6776, a left valve.

Material. Twenty-four valves and several fragments.

Dimensions. Holotype, left valve, Io 6776: L, 0.38; H, 0.18; right valve, Io 6777: L, 0.39; H, 0.19.

Diagnosis. Small, elongate, strong caudal process, surface reticulate, weak longitudinal ridges developed, right valve larger.

Description. Sexual dimorphism cannot be clearly recognized; occasional shorter specimens (0.35 mm) may be females, in which case most of the material consists of males. Although there are not enough specimens to be sure, the right valve appears to be the larger. The surface ornamentation varies in strength between specimens, and is reticulate; there is a tendency for a weak median and ventral ridge to develop. In juveniles the reticulation is more regular, though much weaker, and the surface appears to be punctate. Internally the hinge is as for the genus, the duplicature has a few wavy radial pore canals; the central muscle scars cannot be seen.

Discussion. Externally this is similar to several species now placed in *Semicytherura*: *S. dunkeri* Moos (Melanienion, North Germany), *S. gracilis* (Lienenklaus) (Rupelian, Paris Basin), and *S. oedeleimensis* (Keij) (Eocene–Oligocene). It differs in details of ornamentation and shape, as well as in internal details.

Acknowledgements. I thank Drs. B. Daley and N. Edwards for reading a draft of the manuscript and for valuable discussions. I am indebted to Mr. R. Cumberland (Geology Department, Glasgow University) for running the computer program and to Mr. G. McTurk (Geology Department, Leicester University) for the stereoscan photographs.

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APPENDIX

Details of sampling horizons for Headon Hill (HH) (SZ 305860) and Whitecliff Bay (WB) (SZ 642863) are given in text-fig. 1. Other samples mentioned are: from Headon Hill, HHCP2, *Cyrena pulchra* Bed sample no. 2 (see text-fig. 5); Base of UB, freshwater clay immediately below the Venus Bed; Base V.B., V.B. 18, Mid V.B., Top V.B., samples through the Venus Bed; NHH 1–4, samples from the horizon of HH48 collected in more detail. CB is Colwell Bay (SZ 327878–330890) 1 and 2 from the Oyster Bed, 4–6 from a blue sandy clay with shells 60–200 cm above the Oyster Bed, 12 a thin buff limestone in the Upper Headon Beds near Cliff End; HHL is the Howe Ledge Limestone of Colwell Bay; MF is Milford (SZ 278917), 1 and 2 from the *Unio* Bed, 3 and 4 from the Middle Headon Beds; BC is Bouldnor Cliff (SZ 401920), 3 topmost Bembridge Limestone, 570 cm above the limestone, 8, a further 120 cm higher; BR is Brockenhurst (SU 324036), 1 and 3 from the Middle Headon Beds; Thorness Bay (SZ 464945).

A REVIEW OF THE ECOLOGY OF UPPER CARBONIFEROUS PLANT ASSEMBLAGES, WITH NEW DATA FROM STRATHCLYDE

by A. C. SCOTT

ABSTRACT. Previous studies on Upper Carboniferous floral palaeoecology are reviewed and relationships between fossil plant assemblages, depositional environments, and contemporaneous plant communities are discussed. A point-quadrat sampling technique was applied to a quantitative study of plant horizons in a 'roof shale' of a thin coal below Skipsey's Marine Band (Westphalian B) at a locality near Annbank, Strathclyde. This study has shown that the number and percentage cover of 'drifted' and *in situ* species varies up the succession. Changes in the depositional environment from swampy flood plain to near channel alluvial discharge, interpreted from the lithofacies, are thought to account for these differences by affecting the quantity of plant material deposited and by incorporating a variety of 'Plant Communities' to yield different 'Fossil Plant Assemblages'. The latter consist of two main types, one of pteridosperms with some *Cordaites* and another of sphenopsids and pteridosperms with *Cordaites*. Only very few lycopod remains were found. This is in contrast to the coal-forming swamp 'community' (as seen in the spores contained in the coal) which was dominated by lycopods with some sphenopsids.

A NUMBER of plant communities existed during the Upper Palaeozoic, for example various authors have recognized 'upland' and 'swamp' floras (Cridland and Morris 1963; Havlena 1971; Leary 1974). The relationships, however, of fossil plant assemblages to contemporaneous plant communities and their sedimentary history has received less attention, although a few workers have tried to define more clearly the ecology of these 'floras' (Havlena 1971). Little attempt has been made to relate fossil plant assemblages to depositional environments, which is necessary in order to understand the nature of the assemblages. A number of sampling techniques have been developed by ecologists studying extant floras (Greig-Smith 1964), some of which may be adapted to the fossil situation. The interpretation of the results obtained in the two different examples are fundamentally different.

This paper sets out to review previous work on Upper Carboniferous floral palaeoecology and discusses the application of Recent ecological-sampling techniques to fossils. A 'roof shale flora' of Westphalian B age from Annbank, Strathclyde, Scotland, is taken to illustrate the use of a half-metre square-quadrat technique on cleared bedding planes. The study of the Annbank section is intended to illustrate how detailed analysis of the sediments and flora, together with palynological data from the underlying coal, can give a better understanding of the Coal Measure environment and the possible plant community structure.

PREVIOUS STUDIES ON UPPER CARBONIFEROUS FLORAL PALAEOECOLOGY

Most early work on Upper Carboniferous (mainly Coal Measures) plants has been concerned with general description: new taxa, their botanical affinities, lists of floras,

and considerations of their stratigraphic age (Scott 1906; Arber 1906). Most discussions concerning the nature and origin of coal concerned an *in situ* or drifted theory (Potonié 1899a; Grand 'Eury 1900; Kendall 1922; Bennett 1963). Understandably, as little work had been done on the ecology of extant floras, few workers were concerned primarily with this aspect although occasional observations were noted in passing (Grand 'Eury 1897; Wünsch 1865; Walton 1935; MacGregor and Walton 1948; Jongmans 1955). Most of the reconstructions of Coal Measure swamp vegetation (Westphalian) included known plants together and showed plant reconstructions rather than ecological associations (Geinitz 1855; Potonié 1899b; Noé 1932; Dahlgren 1931); although sometimes the species associations were noted (drawings by Nathorst *in* Magdefrau 1968, by Bertrand *in* Bertrand and Corsin 1950).

Lycopods clearly played an important role in the peat accumulations contributing to formation of coal seams (seen both from the stigmarian seatearths of most Westphalian coals (Logan 1841), and in the abundance of those plants in coal balls (Binney 1868, 1871, 1872, 1875)) but the detailed ecology of Westphalian floras was generally not investigated. Advances in the study of coal petrology (Stopes and Wheeler 1918) gave an impetus to the ecological study of the peat- (coal-) forming floras. The recognition of the major coal constituents (Stopes 1919) and later coal macerals (Stopes 1935) enabled those studying compressions of plants to relate these to their material (Hickling and Marshall 1932, 1933) thus allowing the general type of peat composition of a coal to be identified.

Several attempts have been made to interpret the habitat of Upper Carboniferous plants by comparison of the internal structure with that of extant plants (Thomas 1911; Weiss 1925; Noé 1932; Cridland 1964; Wartmann 1969). It was concluded that lycopods and sphenopsids lived in wetter conditions than pteridosperms and some cordaites (interpreted from root, stem, and leaf structures). Cridland showed (1964) that one type of *Cordaites* had stilt roots which may be compared with those of mangroves. This does not necessarily mean, however, that it occupied the same ecological niche. It would appear that different species of the genus *Cordaites* could live in widely different habitats, from coastal plain (Cridland 1964) to dryer 'upland' (Cridland and Morris 1963; Wartmann 1969). The ecological interpretations of some of these botanical structures are difficult as Chaloner and Collinson (1975) have shown that comparing the structures of Recent and fossil plants is 'fraught with hazards'.

Care must also be taken when arguing detailed ecology between Recent and fossil peat-forming environments (Leclercq 1926; Griffiths 1927; R. Teichmüller 1955) as, although general principles of the environment may be correct, detailed vegetational comparison is not possible (at least with the Upper Carboniferous) (Spackman *et al.* 1966; Habib *et al.* 1966; Habib and Groth 1967; papers in Dapples and Hopkins 1969; Cohen and Spackman 1972; Cohen 1975). The evidence concerning the climatic conditions of the Euramerian coal swamps has been the cause of much debate (Schopf 1974). The interpretations differ widely from a tropical to a temperate climate (White 1931; Friedrichsen 1972; Schopf 1974) although the absence of growth rings in the wood from the Coal Measures (Westphalian) indicates a uniform climate (Chaloner and Creber 1974), perhaps tropical but at least semitropical and

moist (Noé 1932) straddling the equatorial belt (Friedricksen 1972; Chaloner and Lacey 1973).

The first attempt at a quantitative palaeoecological study of the Coal Measure (Westphalian) flora was the pioneering work of Davies (1908, 1920, 1921, 1929 and summarized by North 1935). Davies showed that data collected in both a quantitative and qualitative way was necessary in any serious attempt to unravel Upper Carboniferous shale floras. Davies also showed that the roof-shale floras associated with coal seams varied in terms of variety of species and total quantity of plant material. He noted the change through time of the floras from ones dominated by sphenopsids (in the lower part of the Coal Measure sequence) to ones dominated by pteridosperms (in the upper part). These changes Davies interpreted in terms of a wet flora giving way to a dry flora. These roof-shale floras do not necessarily indicate changes in coal-swamp floras, rather than changes in sedimentary environments, which Davies did not study in detail. North (1935) commenting on these results remarked 'it is necessary to remember that in collecting fossil plants we are not dealing with organisms *in situ*; the plant impressions in the Coal Measure shales are almost always derived from drifted fragments, and it does not necessarily follow that they represent plants identical with those that gave rise to the carbonaceous material of the next subjacent seam; they may have been transported for a considerable distance by the water that carried the mud in which they were ultimately buried and preserved'. Seward (1933) was one of the first to realize the importance of environments of deposition when he wrote, 'we cannot assume that the contemporary vegetation was exceptionally meagre or locally unrepresented merely because no fossils have been found; it may be because the conditions under which barren sediments were formed were not such as were favourable to the preservation of plant fragments'.

Davies (1929) determined a general pattern of change in the Upper Carboniferous floras of South Wales, a theme taken up by Dix (1934) who set up floral zones, using South Wales as her type area, which were later interpreted by R. Potonié (1951, 1952) as changing due to broad climatic shifts affecting the community structure. Subsequently floral zones were established in other areas, such as the United States (Read and Mamay 1964). Patton (1922) showed how, in Recent times, sedimentation, physiographic features, and plant distribution are all interrelated, a theme pursued in a speculative paper by Robertson (1952), who considered the role that plants played in controlling rhythmic sediments. Chaloner (1968) suggested that the two are intimately related; changes in one affecting the other and both being affected by other variables (such as climate).

Following the early work on coal petrology and using her work on the German Brown Coals, Teichmüller (1952; Teichmüller and Teichmüller 1968) proposed relationships between plant assemblages and coal lithotypes of the Carboniferous. This work led to a theory concerning the ecology of peat-forming communities (Smith 1962, 1963). These studies, together with those of Oswald (1937) and Karmasin (1952), led Haquebard and Donaldson (1969) to reach slightly different conclusions concerning relations between floral changes and coal petrographic variations. These authors adopted the terms used by Karmasin (1952) of different swamp environments and related forest-moor type peat to the formation of vitrite and

vitro-clarite with abundant pteridosperms, lepidophytes, and ferns; open moor with subaquatic cannel deposition (and spore-rich durite) and a transitional reed-moor for the deposition of spore-rich clarite formed mainly by sphenopsids. They also considered Oswald's (1937) relations of preservation of plant debris in relation to ground water and recognized 'a terrestrial zone (above the high water mark)' where dry fusite-clarite was formed, 'a telamitic zone (between high and low water marks)' where bright coals would form, and a 'limnic (subaqueous) zone' where dull coals were formed. Again rather different assemblages have been found by Habib (1966, 1968) in the Pennsylvanian of the United States, probably as the general sedimentary environment and ecology is not the same as in Canada or Great Britain. The presence of abundant fusain in coal has caused controversy (White and Thiessen 1913; Stüzer 1929; Crickmay 1935; Marshall 1954; Francis 1961; Komarek 1972). Some believe that fusain represents true charcoal, and is the result of forest fire, because of the similar three-dimensional preservation (unaltered by subsequent compaction and hence a rigidity acquired before or very early in peat formation); a similar temperature of formation as shown by electron spin resonance studies and specific heat determinations; a general resemblance to charcoal, often with fine detail preserved without any sign of fungal or bacterial attack, and finally the fragmentation of the material (Grebe 1953; Terres *et al.* 1956; Harris 1958; Francis 1961; Austen *et al.* 1966; Stach 1968; Alvin 1974; Scott 1974). Others, however, feel that the resemblance to charcoal is only superficial and object to this method of formation because of the abundance of fusain in Palaeozoic coals in relation to those of subsequent eras; the absence of conflagration and drought in tropical swamp areas today and the presence of unaltered resin bodies associated with the fusain, but no alternative satisfactory mechanisms have yet been found (White and Thiessen 1913; Stüzer 1929; Terres *et al.* 1956 for Gondwanan coals; see discussion in Austen *et al.* 1966; Schopf 1975). This controversy remains unresolved.

White (1907, 1908, 1909, 1931) showed that in the topmost Upper Carboniferous and Lower Permian rocks there were representatives of an 'upland' flora. This idea was expanded by Gothan and Gimm (1930) for the European Permian and again later by Gothan and Remy (1957) who recognized a lowland association of *Calamites* and *Pecopteris* and an upland association of *Callipteris* and *Walchia*. Subsequently such upland floras have been recognized extensively throughout the Carboniferous. Cridland and Morris (1963) in the Pennsylvanian of Kansas extended the work of Moore *et al.* (1936) and demonstrated the major differences between Upper Carboniferous upland and lowland floras, the former containing *Taeniopteris*, *Walchia*, and *Dichophyllum*. Daber (1955, 1957) recognized different plant associations in the Viséan and Westphalian of Germany and Havlena (1961, 1970, 1971), working on Carboniferous successions of Czechoslovakia, described both a coal-forming association of plants (Flöznahe) and an association drifted into the coal-forming area (Flözfern). Obrhel (1960), studying the Stephanian successions in Bohemia, noted relationships between plant assemblages and facies and discussed allochthonous and autochthonous plant preservation.

Josten (1961), studying German Upper Carboniferous stratigraphy, noted the presence of definite and repeated cycles of fossil plant assemblages. Following this work Dräbert (1964), in an extensive quantitative study of roof-shale floras from

a sequence of coals which could be traced some distance laterally, found a differentiation of plant associations which he believed to represent actual plant communities. He argued that where the associations have been transported they have the same composition as those which appear to have been preserved *in situ*. He recognized three associations or 'community types': (1) articulate (sphenopsid), (2) pteridosperm, and (3) lepidophyte-cordaite. It was found that above most coal seams the lycophyte-cordaite association was laterally replaced by the pteridosperm association which was itself replaced by the arthrophyte (sphenopsid) association and rarely was the first and last of these associations found in juxtaposition. It is difficult to know to what extent the assemblages were related to the coal-forming swamp itself or whether to other physiographic features of a flood plain or another environment. As well as providing a stimulating study this work contains an important reference source to the German literature. More recent work has not solved the problems raised by this work (Keller 1972), although Pfefferkorn *et al.* (1975) have recalculated the data and compared it with other sites in Europe and America.

Several Russian workers have interpreted the palaeoecology of Upper Carboniferous plant assemblages (Radchenko 1964; Fissunencko 1965; Krassilov 1972). These studies have included both the Karaganda Basin (Oshurkova 1967, 1975) and the Donetz Basin (Stschegolev 1965, 1975; Fissunencko 1967; Fissunencko and Stschegolev 1975). However, this work has been mainly qualitative and only one quantitative study has been published (Oshurkova 1974). Nevertheless three types of plant community have been recognized (Oshurkova 1967): (1) foreshore-hydrous silvan vegetation (waterlogged marginal lake forests), accumulating on coastal plains consisting mainly of arthrophytes (sphenopsids); (2) 'Swampy Silvan' (swamp forest) vegetation in coal-forming areas characterized by lepidophytes (lycopods); and (3) 'woody shrub vegetation', in conditions of well-drained plains consisting mainly of pteridosperms. These broad community-types should be regarded as a hypothesis leading towards the recognition of real communities, rather than as real communities in themselves. This pioneering work will be strengthened as more becomes known of the depositional histories of the rock sequences.

Knight (1974) has shown that in the Sabero Coalfield of Spain there were two distinctive floras within the Stephanian A; firstly a flora associated with the coal-forming environment (Flöznah) where fern species dominated pteridosperm species and secondly a hillslope flora (of younger aspect) in the northern area associated with sandier rocks (Flözfern) where pteridosperm species dominated fern species. A recent discovery of abundant *Sporangiostrobus* together with an abundant associated flora preserved in volcanic ash within a coal seam from the Upper Stephanian of Puertollano, Spain (Wagner and Spinner 1976) gives us for the first time a detailed picture of this important coal-forming community. The spores of *Sporangiostrobus* (micro-, *Densosporites* and mega-, *Zonalesporites*) are known to occur abundantly at many levels in coals of Upper Carboniferous age (Grebe 1966), but until now only a few specimens of the parent plant were known. Associated with this plant in the same ash band, which presumably engulfed and preserved this community *in situ*, are abundant ferns (mainly pectopterids yielding *Torispora*), *Scolecopteris*, sphenopsids (*Asterophyllites* and *Macrostachya*), and cordaites (mainly *Cordaitanthus* with only a few leaves).

There has been renewed interest in various aspects of Upper Carboniferous floral palaeoecology in the United States (Phillips *et al.* 1973). Peppers and Pfefferkorn (1970) examined both macro- and micro-plant remains from a stratigraphic interval in the Carbondale formation, and distinguished qualitatively numerous plant 'associations', related to different physiographic features: 'Wet swampy' with lycopods, ferns, and rare cordaites; 'Dry swampy' with ferns, lycopods, and sphenopsids; 'Levéés and flood plains' with pteridosperms, ferns, and sphenopsids; and 'Upland' with pteridosperms, cordaites, and rare Noeggerathiales. Their schematic interpretation of floral distribution in sedimentary facies has proved useful as a working model, although the basis for some of the ecological interpretation (such as a wet or dry swampy area) remains uncertain.

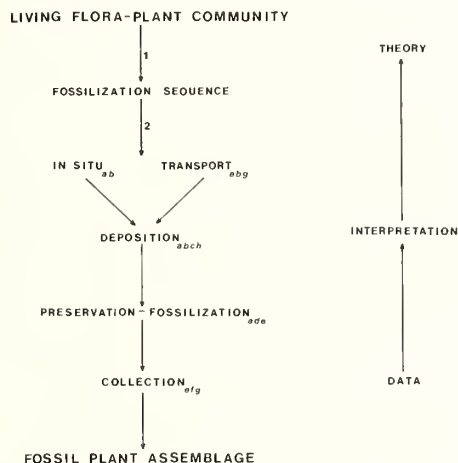
Phillips *et al.* 1974*a* and Phillips *et al.* 1974*b* described the quantitative analysis of coal-swamp vegetation in relation to coal, using the plants present in coal balls as a guide to the constitution of the coal. They have noted that in the Illinois Basin there is a major change in coal-ball floras from the Westphalian to the Stephanian from one dominated by lycopods to one dominated by tree ferns. This change has been interpreted as indicating a broad climatic shift at that time. Darrah (1941) noted that the coal-ball floras from Iowa are dominated by cordaites, pteridosperms, and ferns and so if these floras really represent those plants which formed the coal, as most workers argue, then it would appear that many groups of plants were capable of coal formation and it may have been environmental factors rather than specific communities which were responsible for coal formation, although some were more suited than others. This work is supported by recent advances in coal chemistry (Niklas and Phillips 1974).

The age of the Dunkard Series of the eastern United States (Clendening and Gillespie 1972) is a problem showing the importance of ecology in any palaeobotanical stratigraphical work—see also Oshurkova (1975). Pennsylvanian upland floras have been studied by Leary (1974, 1975; Blazey 1974) who showed a rather different floral composition from the normal swamp flora, which was rich in Pteridospermales and Noeggerathiales and deficient in ferns and lycopods. Although upland floras were recognized as macrofossils early in this century it was not until 1958 that Chaloner (reinterpreting data from Neves 1958) showed that such floras could be recognized in the palynological record. Schopf *et al.* (1944) had commented that some of their conifer pollen might have been produced by upland species (p. 28), but this aspect of their work was not followed up until the stratigraphical distribution of spores had been studied (Smith and Butterworth 1967; Chaloner and Muir 1968; Friedrichsen 1972).

Many workers across the Euramerian coal-forming belt have recognized, particularly in the Westphalian, three major lowland plant assemblages; one dominated by lycopods, one by sphenopsids, and one by pteridosperms as well as various upland floras. It is now important to relate these assemblages to depositional environments with the hope of unravelling the Upper Carboniferous plant community structure.

PROBLEMS IN RELATING FOSSIL PLANT ASSEMBLAGES TO CONTEMPORANEOUS PLANT COMMUNITIES

Ecologists studying living plant associations have long argued over the definition of a plant community and how to characterize it statistically (Greig-Smith 1964), but the fossil plants a geologist finds generally represent the fragmented parts of individuals, often derived from plant communities only brought together by transport and sedimentary processes. Further the plants observed may have undergone changes of one sort or another during the fossilization process (Rolfe and Brett 1969). Problems in relating invertebrate fossil assemblages to their living communities have been discussed extensively over the last fifteen years (see references in Walker and Alberstadt 1975), and have included the study of processes that may affect an organism after death (Taphonomy). Little work concerning macrofloras has been published, although these problems have been recently discussed in some unpublished theses (Hill, Leeds, 1974; Spicer, London, 1975). Krassilov (1969, 1972, 1974) emphasized palaeofloristic successions and their causes, rather than relating fossil plant assemblages to contemporaneous plant communities. Once that data has been collected in a repeatable fashion, then hypotheses concerning possible plant communities will involve the intermediate steps of an interpretation of transport and depositional histories of the plants. These hypotheses may be constantly modified with the collection of new data and also with changes of interpretation of the



TEXT-FIG. 1. Problems in relating fossil plant assemblages to contemporaneous plant communities. 1, Initiators of the fossilization sequence (on some or all of the plants in a community): (i) Internal factors; organ abscission; organ shedding; disease; resistance of plant organ to decay. (ii) External factors; animal destruction; storms; floods; land subsidence; climatic change; erosion; other natural catastrophies, e.g. forest fire, proximity to site of transport. 2, Key to factors controlling fossil plant assemblages (on some or all the plants in the fossilization sequence): (i) Destructive mechanisms; (a) decay, (b) mechanical break-up, (c) immediate post-depositional reworking, (d) diagenesis, (e) weathering, (f) collecting bias. (ii) Interference, (g) sorting, (h) additions from other communities.

sedimentary environments. The major processes involved in the formation of a fossil assemblage are set out in text-fig. 1. Initiators of a sequence are listed under internal and external factors and 'noise' may be related to destruction of all or some of the plants at any stage, or interference by other factors during the major sequence. Text-fig. 1 shows in the left-hand column, those processes which have gone into forming a fossil plant assemblage and in the right-hand column those steps an investigator must take to retrace these paths. This sequence does not interpret the changes in assemblages up a succession but represents primary taphogenic assemblages (those connected with changes affecting plant remains in the course of their transportation and burial, Krassilov 1969).

SAMPLING TECHNIQUES

Numerous sampling techniques have been employed in ecological studies on fossil plants. The merits of different techniques have recently been discussed by Hill (unpublished thesis, Leeds, 1974) and Spicer (unpublished thesis, London, 1975) but those considered here have been used in Palaeozoic studies. Coal Measure palaeoecological studies were pioneered in South Wales by Davies (1908, 1920, 1921, 1929) and this work was continued by Dix (1934). Techniques employed by both authors suffer from subjectivity and so are not reproducible. Much of the quantitative data collected by Davies was obtained by counting the number of plant fragments found at a particular level. No standard sample size was used and genuine changes in floral assemblages are hidden by the nature of fragmentation of each species and their depositional histories. Neither the absolute numbers obtained nor the relative proportions of each species can be compared with those from other horizons. Dix (1934) also failed to use an objective sampling technique but used a subjective method of designating 'dominant' and 'subsidiary' species. Harris (1952), whilst studying the Yorkshire Jurassic, used another type of quantitative method, a measure of frequency (in a sense more or less equivalent to 'fidelity' of ecologists studying Recent plant communities), which he defined as the number of localities at which a species has occurred as a percentage of the total number of exposures of that horizon studied. This use of 'frequency' may be helpful in recording the persistence of species and its use may be extended to the study of Coal Measure plant beds rather than localities or exposures.

Dräger (1964) used a half-metre square quadrat technique, and used in essence the presence or absence of species to record their vertical and horizontal frequency in roof shales. A common technique for Recent ecologists is the quadrat, either by an analysis of cover or frequency determination (Greig-Smith 1964). The interpretation and problems of quadrat analyses on modern plant communities have been reviewed by Frenkel and Harrison (1974). Both the size of quadrat and the type of data obtained from the quadrat are important and are directly related to the type of palaeontological section to be examined, to the type of data required, and to the time available for study. The quadrat size may have to be smaller than ideal, due to the numerous problems in excavation and data collection. The basic counts which can be made from a fossil quadrat are (1) the number of fragments of each species (Hill, unpublished thesis, Leeds, 1974) and (2) the cover area of each species (this paper). The

first method has the problems that the results are greatly affected by the extent to which different species break up during transport and also by the process of sampling itself. However, the cover technique does not take into consideration the degree of fragmentation of the plants, and some plants may be under- or over-represented because of their morphology or because of their uneven scatter on the bedding plane. A cover technique has been used in the example described here, but some assessment of the fragmentation and density of each species was also made.

The sampling technique used at Annbank was as follows:

At each plant horizon a half-metre square quadrat of one or more closely spaced bedding planes was cleared and a grid with 100 random points was placed over the area. The presence and identity of plant remains was recorded underneath each point to give a numerical assessment of the percentage 'cover' of each species on the quadrat; the bare rock was also recorded. When a quadrat could not be conveniently cleared, blocks of one horizon were split and laid out in the quadrat area and then the count was made. Using this method counts of plant, bare rock, and space were made and so extra random points were recorded until the total of plants plus bare rock was 100. There are several factors influencing the results (text-fig. 1). Because of the small extent of exposure the quadrats could not be placed in a random fashion but only where the section allowed. Errors may also occur from the nature of the technique itself and also that only 100 points per quadrat were taken. It is felt that 100 points represents a justifiable compromise between the time taken and the reliability of the results. The way in which a rock splits along the bedding may also influence the results, and it is rarely possible to measure cover on a single bedding plane. This problem is accentuated by the presence of plants such as *Cordaites* whose typically large strap-like leaves increase the probability of the rock cleaving open wherever they occur. In a given volume of rock, therefore, containing some *Cordaites* but perhaps a greater quantity of smaller parts of other plants, the rock will cleave preferentially to expose the *Cordaites*, resulting in some bias favouring such large plant parts.

This use of 'cover' differs from that used by plant ecologists in a living community. There one is measuring the result of interactions between the plants, e.g. the extent to which a species is successfully using the light for photosynthesis. In the fossil (death) assemblages there is no interaction of assembled species and the percentage cover is merely a measure of area of plants (leaves and stems which were originally upright before transport) on the rock surface exposed by splitting. It is probably the easiest parameter to measure related to the mass of plant material contributed by any constituent of the community(ies) from which the assemblage was derived, as well as being related to the total photosynthetic surface of the plant in life—which is related to its status in the living plant community. The 'cover area' of each species, therefore, is related in part to its original biomass, in part to its preservability, and in part to its hydrodynamic qualities. Such a cover area is a measure of its 'thanatomass'. Some plants may have a high thanatomass but may have been small contributors to a community whilst others such as ferns may have had an important role in a plant community and perhaps a large biomass, but because of the relative ease with which they are broken up they may have only a small thanatomass in a fossil plant assemblage.

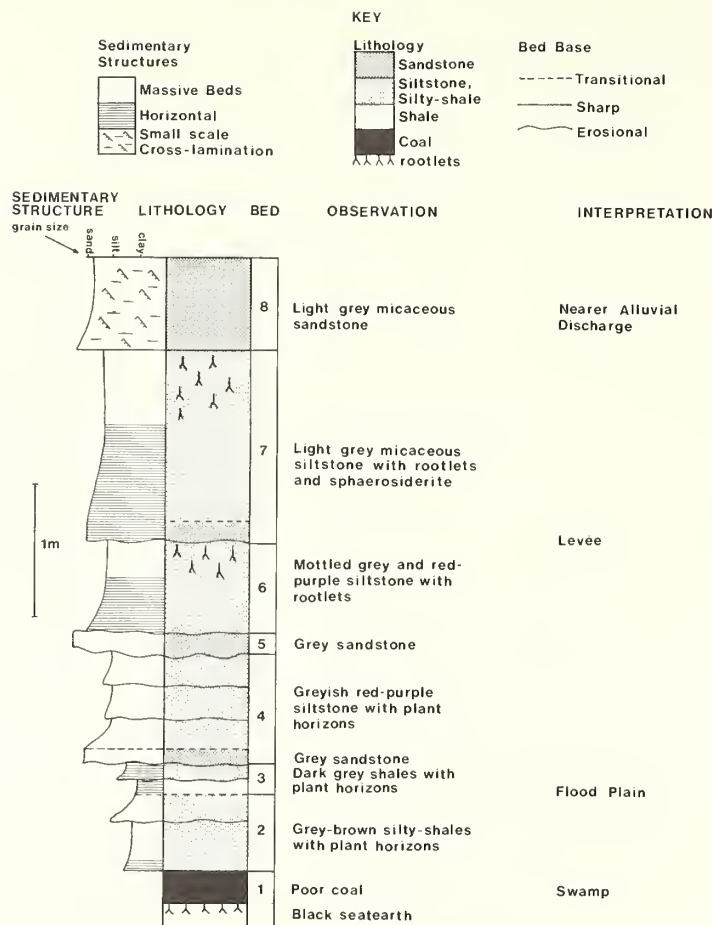
Few of the plant beds were sufficiently thick to enable more than one quadrat to be carried out through it. The section at Annbank exposed 10 m of sediment laterally in the banks and no quantitative work could be done on the lateral distribution of species as well as the vertical distribution. Estimation of the fragmentation of each species at each level was undertaken when recording quadrats. At some levels, i.e. Bed 2a, text-fig. 3, the plants showed a preferred orientation but this was not so for every horizon. Measurements could only be carried out on some levels because of the necessity of removing blocks of a bed from the bank for examination. Semi-quantitative cover abundance scales have been widely used by ecologists studying extant plant communities for quick estimation of quadrat, and hence cover, values. Two scales are in general use, the Braun-Blanquet Scale (1-5) and the Domin Scale (1-10). Both scales use a combination of statistics, i.e. both frequency and cover value. The cover values obtained during this study have been converted to the Domin Scale and are shown in Table 1. This has the advantage of showing up changes in members of the flora which may be numerous but because of their size and shape always record very low cover abundance (e.g. *Annularia*).

AN ECOLOGICAL STUDY OF A WESTPHALIAN ROOF-SHALE FLORA

Fossil plants from the Coal Measures of Annbank, Strathclyde have been previously recorded by the Geological Survey (Eyles *et al.* 1949, p. 93). The locality is 'on the left bank of the River Ayr opposite the village of Annbank just south of the piers of an old bridge' (NS 400 234). Stratigraphically it is considered to lie between the Top Ell Coal and Skipsey's Marine Band (Top Westphalian B, Eyles *et al.* 1949, p. 93). Subsequent mapping of the Carboniferous rocks of the area (Mykura 1967) failed to reveal any further information about this locality. The locality has been re-examined and the section described and recorded in lithographic log form, text-fig. 2 (Selley 1970) and the plants have been studied using the quadrat technique described above. Other species were examined from this locality in the collections of the Geological Survey of Edinburgh and the Hunterian Museum, Glasgow. A palynological investigation of the coal was also undertaken to compare with the compression (Walton 1936, p. 220) flora in the roof shales.

SECTION DESCRIPTION

Lithology. The strata exposed in the river bank consists of 5 m of sediments dipping 10° north at 120° (text-fig. 2). At the base of the section, 12 cm of coal (Bed 1), mainly shaley but bright in part is underlain by a dark grey to black micaceous seatearth with stigmarian rootlets. Resting on the coal are 75 cm of grey silty shales (Bed 2), consisting of eleven upward-fining units, each of which generally has abundant plant material at the top (text-fig. 3). The top unit grades into a fine black shale (Bed 3) with abundant plants and *Pinnularia* (small detached roots showing extensive branching) at one level. The base of the next bed (Bed 4a) is a slightly erosive red (iron-rich, haematitic) silty-sand which is followed by three upward-fining sequences of reddish-grey siltstones, laminated at the top with plants, and very iron-rich in parts. Above these rocks is a grey micaceous fine sandstone with an erosive base (Bed 5), followed by grey micaceous silty shales laminated at the base. These pass into mottled red and green micaceous silts which contain numerous rootlets (not *Stigmaria*) consisting of leached brown traces. This horizon is followed by a micaceous siltstone, finely laminated at the base and passes into light-grey micaceous siltstone with small rootlets and abundant, dispersed sphaerosiderite. There is then a sharp planar erosional

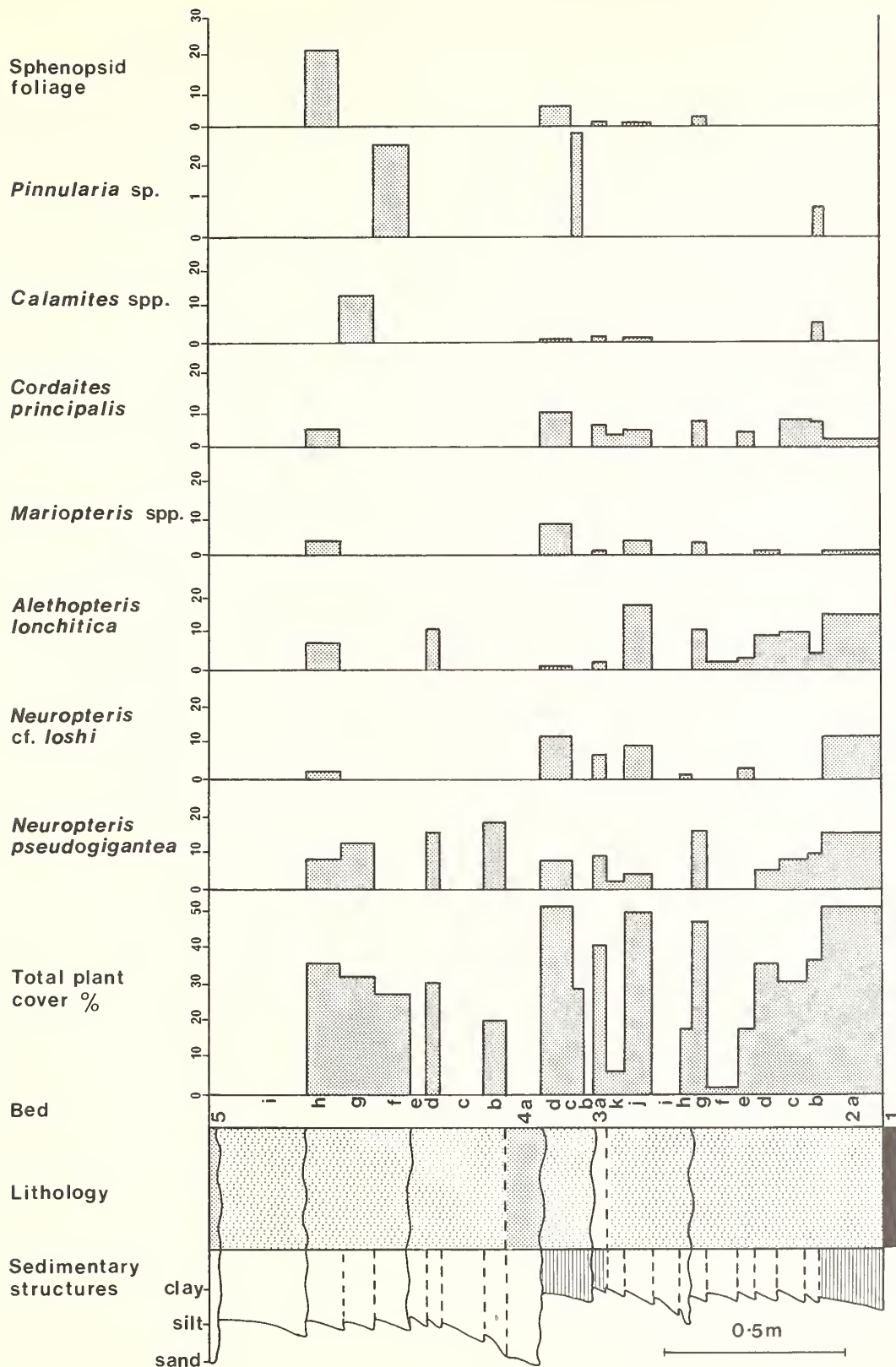


TEXT-FIG. 2. The Annbank Section, with possible interpretations.

base followed by a reddish-grey coarsely micaceous fine sandstone which exhibits small-scale cross-lamination. The Geological Society of America rock-colour chart (1970) was used for the rock-colour descriptions and the grain size was measured in thin section (using the Standard Wentworth Scale).

Plant horizons. The occurrence and distribution of the plants at Annbank is shown in Table 1. The cover variation of the major elements of the flora is shown in text-fig. 3. Owing to limited exposure little quantitative work on lateral variation in the plant horizons could be carried out. Although this did not seem considerable, the possibility of variation was considered when interpreting the significance of vertical changes. The plants occur mainly in the upper part of each upward-fining unit giving it an appearance of having a laminated top but this may be due to the abundance of flat-lying foliage which allows the rock to be easily split.

The basal horizon is a black micaceous seatearth which contains numerous rootlets of *Stigmara* (a lycopod). This seatearth grades into a shaley coal and then a bright coal; this sequence is then repeated, before being followed by medium-grey micaceous silty shales with plants. There is a general increase in the pteridosperm foliage (*Neuropteris*, *Alethopteris*, *Mariopteris*, etc.) with decreasing grain size of rock (Beds 2 and 3) which may be interpreted in terms of both the hydrodynamic properties of the fern-like foliage and the original composition of the assemblage (Ferguson 1971). Part of the assemblage will not



TEXT-FIG. 3. Percentage cover of major plant constituents in the lower part of the succession at Annbank.

be identifiable in the coarser lithology, because the finer details of the plants are not preserved or the plants consist of comminuted fragments. The sphenopsid foliage is first found in Bed 3 and becomes more conspicuous up the succession as do layers containing abundant *Pinnularia* (interpreted as roots of *Calamites*, Crookall 1969) and *Calamites* (pith casts). There is also, consistently throughout the succession, some *Cordaïtes*. No plants were found above Bed 4 other than a few unidentifiable rootlets (but not *Stigmara*) in Beds 6 and 7. There is, in the upper part of the succession, a small correlation between the presence of sphenopsid foliage and a large total percentage cover of plants (fig. 3).

Notes on the status of some plants

(i) *Cordaitanthus* sp. Plate 50, figs. 1–3 (Pb 4457, Pb 4458).

Two specimens referable to the genus *Cordaitanthus* Feistmantel were collected from Bed 2a. *Cordaitanthus* Feistmantel, 1876 takes priority over *Cordaianthus* Grand'Eury, 1877 (Fry 1955) even though the latter is a *nomen conservandum* over *Botryoconus* Goeppert (International Code of Botanical Nomenclature 1972). These two specimens are considerably larger than most previously described from Britain, the closest species being *C. nostellensis* (Barker) 1943 (in Barker and Whittle 1943) and may represent a new species, although no name will be proposed until more specimens are obtained.

Description. Inflorescence in a compound 'catkin', a long narrow axis. Dwarf shoots (Crookall 1970; Florin 1950 = flowers Florin 1950 = buds Barker 1943) are alternate and distichously arranged, diminishing in size towards the apex of the axis. The dwarf shoots are formed of rounded triangular scales and are subtended by a long bract. These inflorescences are associated with the leaves of *Cordaïtes principalis* Germar and the seeds *Samaropsis pyriformis* Barker.

TABLE 2. Dimensions of *Cordaitanthus* spp. (in mm).

	<i>C. sp. (1)</i> (Pb 4457)	<i>C. sp. (2)</i> (Pb 4458)	<i>C. nostellensis</i> (Barker)
Number of dwarf shoots (buds)	5	5	13
Axis length preserved	30	40	138
Axis breadth (max.)	3	3.5	1–5.5
Dwarf shoot length	15	14	19
Dwarf shoot breadth	8	8	15
Scale length	6	?	10
Scale breadth	4	?	3
Bract length	20	?	?

(ii) *Samaropsis pyriformis* Barker, 1944. Plate 51, fig. 14 (Pb 4469).

These seeds, found in association with *Cordaitanthus* sp. (cf. *nostellensis*) have only been previously recorded by Barker 1944—the types from Nostell Brickworks, low Westphalian C, which were found in association with *C. nostellensis* (Crookall 1976). The size range of the Annbank specimens are very comparable (Table 3) being winged seeds with a nucule, cordate-acute, with shallow basal concavity, and a long narrow micropylar tube.

TABLE 3. Dimensions of *Samaropsis pyriformis* Barker (in mm).

	Type specimen	Annbank (Pb 4469)
Total length	13.5	14
Total breadth	9	9
Basal concavity—length	6.5	7
Basal concavity—breadth	7	6
Micropylar tube—length	4 (up to 6 if restored)	6
Micropylar tube—breadth	0.65	0.75

(iii) *Cordaïtes principalis* Germar. Plate 50, figs. 4, 5 (Pb 4459).

These large strap-like leaves are frequent at Annbank, often reaching 5 cm in width and 50 cm in length. Very few apices are preserved and the leaves have tended to break up parallel (during transport) to their margin into ribbon-like strips (Crookall 1970). No cuticle was preserved.

(iv) *Mariopteris* cf. *sauveri* (Brongniart). Plate 51, fig. 7 (Pb 4444).

Numerous specimens of this species were collected, all fairly fragmented. It differs from *M. nervosa* (Brongniart) in that the venation, where seen, is delicate and relatively dense, the apices of pinnules rounded to obtuse and differs from *M. muricata* (Schlotheim) in its pinnule margins not having basiscopic incisions and there being a length/width pinnule ratio of 1.5:1.0 instead of 2.5:1.0 (see Boersma 1972). It may be pointed out that these specimens do resemble apical parts of secondary pinnae of *M. muricata*, and both this species (Pl. 51, fig. 11) and *M. nervosa* occur at Annbank. The possibility exists that all this foliage belongs to one species but it is felt that there are sufficient differences to justify specific separation.

(v) *Alethopteris lonchitica* auct. (*non* Schlotheim?). Plate 51, figs. 1-3, 11, 12 (Pb 4449, Pb 4462, Pb 4446).

A large number of specimens showing a wide range of morphology was found at Annbank. It is believed that these fragments represent different parts of fronds as seen in a more complete specimen figured by Crookall (1955, pl. X, fig. 1). A lot of confusion surrounds this species and the range of morphologies fit with those originally described as *A. urophylla* Brongniart. The name *A. lonchitica* will be retained until there is a revision of this species.

(vi) *Sphenophyllum cuneifolium* (Sternberg). Plate 51, fig. 6 (Pb 4443).

Included with *S. cuneifolium* is its variety *S. cuneifolium* var. *saxifragifolium* (Sternberg) which is considered to belong to the same plant (Crookall 1969).

(vii) *Neuropteris pseudogigantea* H. Potonié. Plate 51, fig. 13 (Pb 4440).

This species has recently been described from the French Westphalian as *Paripteris pseudogigantea* (Potonié) by Laveine (1967). It is a common British species, often confused with *N. gigantea* Sternberg, the latter having much more arcuate and tapering pinnules. The Annbank specimens (mainly isolated pinnules) may be compared with *N. (Paripteris) linguaefolia* P. Bertrand in having very straight-sided pinnules. The two species *N. pseudogigantea* and *N. linguaefolia* in France, have similar stratigraphic ranges—mid Westphalian B to Westphalian C (Laveine 1967).

Palynology. Another 'view' of the flora may be gained by examining the rocks, especially the coals where no macroplants can be identified, for spores and pollen of plants. Many of these spores are known from fructifications which have been examined *in situ* (Courvoisier and Phillips 1975) so it is possible to some extent to gain a compositional view of the flora from this study. However, the relative spore production of each type of plant presents a major difficulty as some, e.g. *Lepidodendron*, produced vast numbers of microspores whereas others such as pteridosperms seemed to have produced fewer but larger. The transport and sorting of these assemblages presents another problem although it is generally considered that the spore composition of a coal gives a good quantitative estimate and certainly a good qualitative view of the coal-forming flora (Smith 1963). The botanical affinities of many of these spores are known (see Potonié 1962 *et seq.*) but the spore genus or species does not necessarily correspond with a macrofossil genus or species, i.e. one cone may contain a variety of spore morphologies, which may be regarded as a number of different spore genera, or else one type of spore may be known from a variety of different plants.

Spore preparations of a channel sample of coal was undertaken. This was macerated using Schulz's solution followed by dilute ammonia (Smith and Butterworth 1967). The spores were mounted on five slides in glycerine jelly and 200 spores were counted on each in order to overcome sorting problems in slide preparation (Chaloner and Orbell 1971). Only genera were recorded in order to give a general view of the spore spectrum. There are many *Lycospora* as well as other spores known to have been produced by lycopods (*Crassispora*, *Endosporites*). The next most abundant group of spores are those produced by

sphenopsids (Table 4). It is striking that the data obtained from the roof using macrofloras is so different from that obtained from the spores composing the coal. If the spores represent the *in situ* flora, as most people believe, then peat forming must have stopped before the inundation of detritus bringing with it the pteridosperm assemblage or else one would expect more macrofossil evidence of lycopods. If, however, the spores represented a more regional picture of the coal-forming flora then these spores would have been transported into this environment. The former explanation is preferred as there is little evidence of lycopods in the roof of the coal and yet it has a stigmarian seatearth.

TABLE 4. The spore composition of the Coal (Bed 1) and their natural affinities.

LYCOPODS. <i>Lycospora</i> 39%, <i>Crassispora</i> 6%, <i>Endosporites</i> 4%, <i>Cristatisporites</i> present < 1%, <i>Densosporites</i> < 1%, TOTAL 49%.
ARTICULATES. <i>Laevigatosporites</i> 23%, <i>Calamospora</i> 13%, TOTAL 36%.
FERNS. <i>Raistrickia</i> 2%, <i>Leiotriletes</i> 1%, TOTAL 3%.
PTERIDOSPERMS. <i>Schopfipollenites</i> < 1%.
CORDAITES. <i>Florinites</i> 2%, TOTAL 2%.
CONIFERS. <i>Potonieisporites</i> < 1%.
UNKNOWN AFFINITY. <i>Dictyotriletes</i> < 1%, <i>Vestispora</i> < 1%, <i>Cingulizonates</i> < 1%, Unknown 10%.

The affinities of spores were taken from Potonié and Kremp (1954) and Potonié (1962, 1965).

Stratigraphical significance of the flora. Of the twenty-six species of plant recorded only four are considered overall to be abundant and six, common. The stratigraphical ranges in Western Europe of these plants are shown in Table 5. From this it may be said that the flora is considered to be of a Westphalian B age.

TABLE 5. The ranges of the most common Annbank plants through the North-west European Westphalian (from Stockmans 1962; Crookall 1939, 1955; Dix 1934; Josten 1971a, b; Boersma pers. comm.). The first four are abundant, the remainder common. r = rare.

	Westphalian			
	A	B	C	D
<i>Neuropteris loshi</i>	×	×	r	
<i>N. pseudogigantia</i>		r	×	×
<i>Alethopteris lonchitica</i>	×	×	r	r
<i>Cordaites principalis</i>	×	×	×	×
<i>Annularia radiata</i>	×	×	×	r
<i>Mariopteris saueri</i>		r	×	r
<i>M. muricata</i>	r	×	×	
<i>Calamites cisti</i>	×	×	×	×
<i>Asterophyllites equisetiformis</i>	r	×	×	×
<i>Sphenophyllum cuneifolium</i>	×	×	r	r

EXPLANATION OF PLATE 50

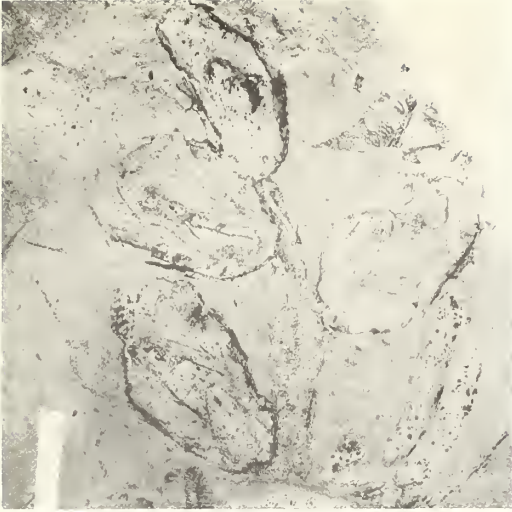
Fossil plants from the Coal Measures of Annbank, Strathclyde.

Figs. 1, 2. 1, *Cordaitanthus* sp., under xylene, $\times 1\frac{1}{2}$, Bed 2a, Pb 4457a. 2, same specimen, top illumination, $\times 1\frac{1}{2}$.

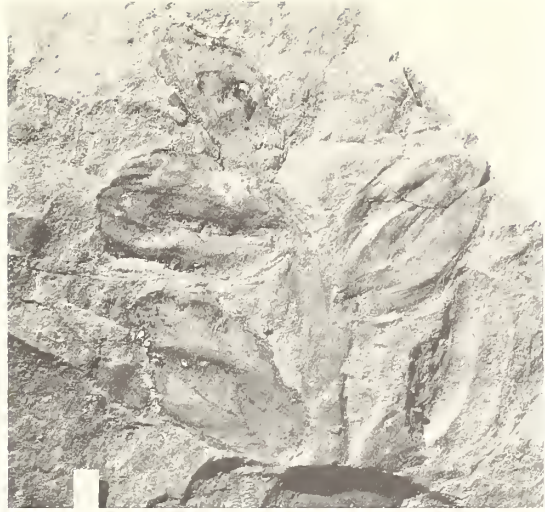
Fig. 3. *Cordaitanthus* sp., under xylene, $\times 1\frac{1}{2}$, Bed 2a, Pb 4458.

Figs. 4, 5. 4, *Cordaites principalis*, $\times 1\frac{1}{4}$, top illumination, Bed 2, Pb 4459. 5, same specimen, top illumination, $\times \frac{1}{3}$.

All the figured specimens are in the Hunterian Museum, Glasgow (Pb).



1



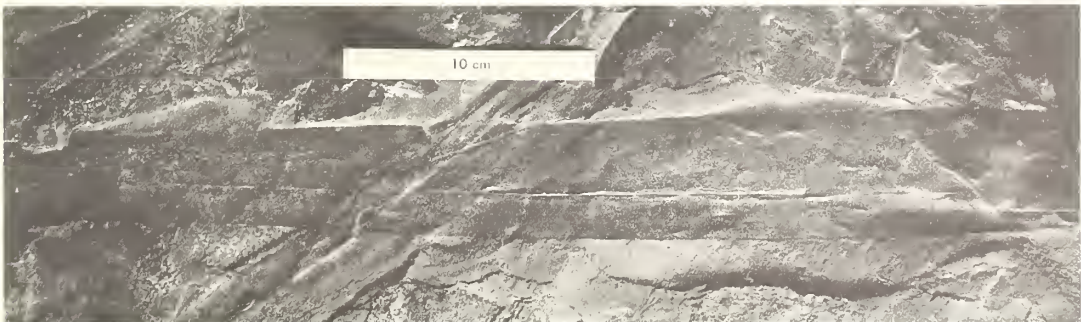
2



3



4



5

SCOTT, Coal Measure plants from Ayrshire

probably from high in the stage. The stratigraphical use of plants in the Upper Carboniferous has been the subject of many papers, notably by Dix (1934) and Crookall (1938, 1955). Other workers have also dated rocks by floras (Stockmans 1962; Josten 1971*a, b*; Novik 1969), and in America similar studies have been made leading to the recognition of Floral Zones (Read and Mamay 1964; Cridland *et al.* 1963). A wide collection of plants from many lithologies must be made to obtain a representative number of species to date a flora. As only genera of spores were identified they were not used in the stratigraphical determination, although Smith and Butterworth (1967) have set up palynological zones which are useful when there is no macrofossil flora or fauna, or to back up the data obtained from those groups. The great contrast between the flora, represented by spores from the coal, and the flora represented by macrofossils, from other lithologies, and their subsequent interpretation, might help explain the difficulty in matching Smith and Butterworth's (1967) spore zones and Dix's (1934) macrofossil zones.

The depositional environment. Depositional environments in the British Coal Measures have been reviewed by Duff *et al.* (1967), Hemingway (1968), and Elliott (1968, 1969), and facies analysis of West European sequences have been made by Reading (1970, 1971). These sequences may be compared to Recent peat-forming environments, and although detailed correlations are not possible, broad outlines have emerged (Fisk 1960; symposium papers in Dapples and Hopkins 1969; Coleman 1966; Reineck and Singh 1973). The succession at Annbank consists, at the base, of numerous small upward-fining units of micaceous silty shales and shaley silts with abundant plant fragments at the top of each, resting on a coal, shaley in part, underlain by a dark micaceous seatearth with *Stigmara* (the bases of lycopods). Coal with an underlying seatearth represents an *in situ* peat deposit produced by 'swamp' vegetation (Elliott 1969). The area was subsequently inundated with detritus in irregular pulses which gave rise to each small upward-fining unit incorporating plant remains. This sediment may have been introduced in two ways: (1) by direct stream discharge into a now shallow lake or, (2) by the flooding of the swamp area by levée bank break (crevasse splay).

The lithologies above Bed 3 take on a coarser aspect and the *Pinnularia* horizons may have resulted from sphenopsids rooting in the sediment. These units are interpreted as being closer to the possible site of alluvial discharge. The mottled silty

EXPLANATION OF PLATE 51

Fossil plants from the Coal Measures (Westphalian B) of Annbank, Strathclyde.

- Fig. 1. *Alethopteris lonchitica*, $\times 1$, top illumination, Bed 4h, Pb 4449.
 Fig. 2. *Alethopteris lonchitica*, $\times 1$, under xylene, Bed 2j, Pb 4462.
 Fig. 3. *Alethopteris lonchitica*, $\times 3$, detail of fig. 2.
 Fig. 4. *Neuropteris cf. loshi*, $\times 3$, under xylene, Bed 3d, Pb 4454.
 Fig. 5. *Mariopteris muricata*, $\times 3$, detail of fig. 9, Bed 3, Pb 4465a.
 Fig. 6. *Sphenophyllum cf. cuneifolium*, $\times 2$, under xylene, Bed 4h, Pb 4443.
 Fig. 7. *Calamites cisti*, $\times 1$, top illumination, Bed 4g, Pb 4450.
 Fig. 8. *Mariopteris aff. saueri*, $\times 1$, top illumination, Bed 4h, Pb 4444.
 Fig. 9. *Mariopteris muricata*, $\times 1$, under xylene, Bed 3, Pb 4465a.
 Fig. 10. *Trigonocarpus* sp., $\times 1$, top illumination, Museum Collection Pb 4540.
 Figs. 11, 12. 11, *Alethopteris lonchitica*, $\times 1$, top illumination, Bed 4h, Pb 4446. 12, detail of fig. 11, $\times 13$.
 Fig. 13. *Neuropteris pseudogigantea*, $\times 3$, top illumination, Bed 4b, Pb 4440.
 Fig. 14. *Samaropsis pyriformis*, $\times 3$, under xylene, Bed 2d, Pb 4469.
 Fig. 15. *Asterophyllites equisetiformis*, $\times 1$, under xylene, Bed 4h, Pb 4442.
 Fig. 16. *Annularia radiata*, $\times 1$, under xylene, Bed 4h, Pb 4441.

All the figured specimens are in the Hunterian Museum, Glasgow (Pb).



SCOTT, Coal Measure plants from Ayrshire

sands with abundant rootlets (not stigmarian) and disseminated sphaerosiderite have been taken as an indication of frequent water-level change and exposure to the air (Elliott 1969) with resulting colonization by plants (possibly sphenopsids such as *Calamites*). There are alternative interpretations for the deposition of these rocks. With the stream (river) discharging into a shallow swampy lake, rapid silting up would take place (providing there was no subsidence), which would lead to colonization by plants with the periodic drainage (the intervals between flooding) causing rise and fall on the water table and frequent subaerial exposure. Alternatively, if the sediments represent genuine overbank deposits, then the sediments would coarsen towards the stream bank, and the coarser sediments with frequent exposure may represent actual levée deposits. These deposits are succeeded by small-scale cross-laminated fine micaceous sandstones. Such sequences have been reviewed by Allen (1965) and are also similar to many of the intradeltaic sequences of Elliott (1969). The two different hypotheses for the depositional environment of Beds 2 to 8 make the interpretation of the plant assemblages contained within them more difficult. The coal contains abundant lycopod spores which may have come from plants which lived *in situ* in the swampy peat- (coal-) forming environment or else may have been transported and deposited in that area. The palynology of coal-seams (Smith 1962) indicates that the spores chiefly represent the flora of the coal-forming community, although not necessarily the actual 'on-the-spot' composition. If this interpretation is correct for Annbank, then peat formation must have stopped in the area before the inundation of shaley-silts containing foliage of the pteridosperms *Neuropteris* and *Alethopteris*, since no lycopod remains are found in any of the units immediately above the coal. It is unlikely that if the lycopod vegetation was still thriving in the 'swamp' area during the initial flooding and sediment discharge, none of it would have been incorporated into the basal silty layer although much of it might have been transported out of the area. This discrepancy between the topmost coal flora and the roof-shale flora is frequently encountered in north Britain although occasionally abundant lycopod remains are found in roofs of shaley coal (Penny Hill seam, Ragpath, Co. Durham) and occasionally abundant upright trunks (Jongmans 1955; roof of Barnsley Top soft coal, Lowther North, near Wakefield) are preserved. Therefore the flora in the basal silty shales represents an assemblage of pteridosperm foliage with some *Cordaites* which may be the result of incorporation in detritus deposited by flooding or discharge into the area by a river or river system. The two hypothetical depositional environments postulated, although broadly similar, give rise to two hypotheses concerning the derivation of the plant assemblages from original plant communities. If the pteridosperm assemblage was deposited directly by a river into a shallow lake then the plants may have come from various sources; either from the edges of the swamp, lake, river banks, or from upstream. It is difficult to know from the fragmentation how far the plants have travelled. They do not appear to have travelled far, but Ferguson (1971) has shown that leaves may travel a considerable distance, even up to 50 km, without much damage, and even a few kilometres may encompass a wide variety of communities. The silting up of this shallow lake might have been accompanied by the colonization of mainly sphenopsids with some pteridosperms.

If the sediments were deposited by crevasse splay on to a floodplain then there

are other possible derivations for the plant assemblages. This detritus would include fragments of plants living around the swamp edge as well as perhaps some fragments of plants which had been incorporated in the sediment before flooding. Each pause in sedimentation would allow many of the plants to re-establish themselves on the floodplain only to be incorporated by the next flood. With meandering streams or rivers across the floodplain and a number of flooding episodes, levée bank deposits would be built up, upon which sphenopsids, such as *Calamites* might have grown, which would have been incorporated into the alluvium during flooding episodes. It is uncertain how *Cordaite*s lived. The genus has been considered a pathological xerophyte (Wartmann 1969), as possibly inhabiting coastal plains (Cridland 1964; Peppers and Pfefferkorn 1970), or else living in the 'uplands' (Chaloner 1958; Peppers and Pfefferkorn 1970), which may have only been 10 m in height (Cridland and Morris 1963, p. 79). The occurrence of *Cordaitanthus* with long slender bracts in the basal silty shales (Pl. 50, figs. 1-3) would not indicate long transport as it would tend to break up easily.

CONCLUSIONS

Previous Upper Palaeozoic floral palaeoecological studies have shown the presence of three major swamp or lowland associations: lycopod, sphenopsid, and pteridosperm (Havlena 1971). However, there is not sufficient quantitative or sedimentological data to interpret these associations in terms of the plant communities from which they were derived. A quantitative study, using a point-quadrat technique, of a 'roof-shale' flora from the Westphalian B of West Scotland together with sedimentological observations and palynological data from the underlying coal has also shown the presence of such plant assemblages. The flora forming the coal is considered to represent an *in situ* community (as seen by the palynology) dominated by lycopods and sphenopsids. The roof-shale flora in contrast consists of two main assemblages; a lower one of mainly Pteridosperm foliage (*Neuropteris*, *Alethopteris*, and *Mariopteris*) with some *Cordaite*s and an upper one which has in addition numerous Sphenopsids (*Calamites*, its foliage *Annularia* and *Asterophyllites* and its roots *Pinnularia*, as well as *Sphenophyllum*). These assemblages represent drifted accumulations, and the composition of these floral assemblages in terms of quantity of plant material and species content will be affected by both the different plant communities, or selections from them, which are being incorporated into the sediment, as well as the depositional history of the rocks themselves. The difference between the coal-forming flora and the roof-shale flora is emphasized. As the factors governing fossil plant assemblages are complex, their interpretation in relation to the fossil plant communities from which they have come is necessarily speculative. Changes, therefore, in the interpretation of the depositional environment of the plants, and their sedimentary history, must involve reconsideration of any plant-community model.

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A NEW FAMILY OF PALAEOZOIC OSTRACODS

by M. N. GRAMM

ABSTRACT. The family Egorovitinidae is erected for *Egorovitina kirssanovi* gen. et. sp. nov. a new ostracod with an unusual adductor muscle scar, from the Lower Carboniferous (Visean) deposits of the Novgorod region, U.S.S.R. The presence of a simple calcified inner lamella may indicate that this new family has affinities with the Podocopina.

IN the Lower Carboniferous, Viséan strata (Alexinsky horizon) of Novgorod region (Borovitchi district) some carapaces and valves of a new ostracod species *Egorovitina kirssanovi* gen. et sp. nov. have been found.

The adductor muscle scar is of an extraordinary pattern (text-fig. 1). It resembles a five-toed footprint consisting of a postero-median or postero-ventral spot with five elongate anterior spots arranged in a pedate pattern.

The discovery of this structure increases the number of Palaeozoic ostracod groups whose adductor muscle-scar patterns were highly ordered. Previously this has been demonstrated on *Scrobicula scrobiculata* (Jones, Kirkby and Brady) (see Gramm and Posner 1972). It shows that the adductor muscle-scar patterns of Palaeozoic ostracods do not in all cases consist of an irregular cluster of randomly arranged spots.

On account of this unusual adductor muscle-scar pattern the new family, Egorovitinidae, is erected. The ordinal position of the new family is unclear. It is doubtful whether at present the problem can be solved by means of the adductor muscle scar. The adductor pattern shows that Egorovitinidae fam. nov. cannot be included in the suborders Platycopa and Metacopa, or amalgamated with the known families of Podocopa. Contrary to this a quite indefinite position exists about the interrelation with Palaeocopida (= Beyrichiida), because the scarcity of the adductor muscle-scar data prevents any comparison. At the same time propinquity to the Palaeocopida (= Beyrichiida) should be excluded on the basis of the carapaces outlines, straight (not convex) ventral margin, and surface without sulcation and lobation of the new family.

A very important criterion is the calcified inner lamella. In the material studied it is of primitive type resembling that in *Scrobicula* and *Roundyella* (Gramm 1976), i.e. thin, narrow, and of a uniform width along the entire free margin. According to this structure the family is tentatively attributed to the suborder Podocopina.

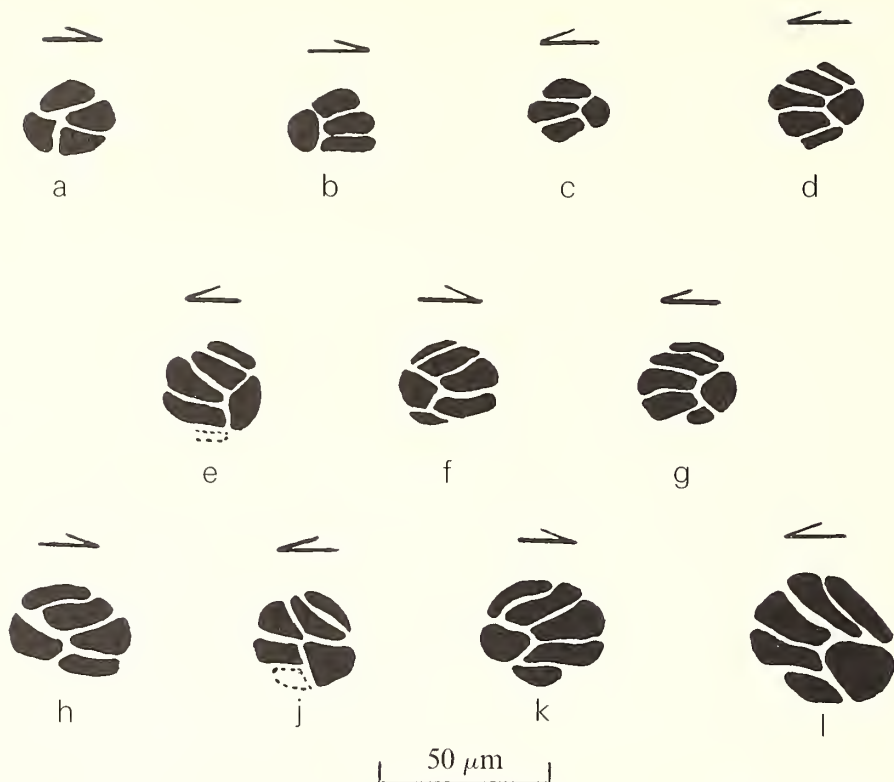
All specimens referred to in the text under Nos. 1116 and 1126 have been deposited in the Institute of Biology and Pedology, Far-East Scientific Centre, U.S.S.R. Academy of Sciences, Vladivostok.

SYSTEMATIC DESCRIPTION

Suborder ?PODOCOPINA Sars, 1866

Family EGOROVITINIDAE Gramm, fam. nov.

Diagnosis. Carapace elongate, subrectangular, with ridge-like swellings along both extremities. The circular adductor muscle scar consists of a postero-median or



TEXT-FIG. 1. Adductor muscle scars of different growth stages of *Egorovitina kirssanovi* gen. et sp. nov. from the Lower Carboniferous, Viséan, Alexinsky horizon, Borovitchi district, Novgorod region, U.S.S.R. *a*, right valve external view, 1126/9-3 (L = 275 μ m). *b*, right valve external view, 1126/10-1 (L = 275 μ m). *c*, left valve external view, 1126/10-2 (L = 285 μ m). *d*, right valve internal view, 1126/1-4 (L = 325 μ m). *e*, left valve external view, 1126/9-2 (L = 325 μ m). *f*, right valve external view, 1126/10-3 (L = 330 μ m). *g*, left valve external view, 1126/10-4 (L = 330 μ m). *h*, left valve internal view, 1126/1-2 (L = 360 μ m). *j*, right valve internal view, 1126/7-2 (L = 385 μ m). *k*, left valve internal view, 1126/1-1 (L = 400 μ m). *l*, right valve internal view, 1116/124 (L = 475 μ m). L—length of valve. Arrows indicate anterior.

postero-ventral spot with five elongate anterior spots, of which the three middle are the longest. Calcified inner lamella of primitive type.

Assigned genera. *Egorovitina* gen. nov. from the Lower Carboniferous deposits of Novgorod region.

Remarks. See generic description.

Genus EGOROVITINA nov.

Derivation of name. In honour of Dr. G. I. Egorov, a student of Palaeozoic ostracods from the North-Western regions of the U.S.S.R.

Type species. *Egorovitina kirssanovi* sp. nov.

Diagnosis. Carapace small, elongate, thin-walled, subrectangular in outline. The left valve is larger. Both extremities broadly rounded, the posterior higher than the anterior. Dorsal margin straight, ventral nearly parallel to it. Along the extremities are ridge-like swellings (ridges); in the antero-ventral/postero-dorsal parts of the right valve, and in the postero-ventral/antero-dorsal parts of the left valve these form prominent elongate knobs. Surface with shallow smoothed pits. Hinge adont. Inner calcified lamella thin, narrow and of uniform width, with a contact groove on the left valve. Radial pore canals not observed. Normal pore canals very thin, numerous. The adductor muscle-scar pattern as for the family.

Assigned species. Only the type species.

Remarks. The outline of the new genus resembles *Roundyella* Bradfield, 1935. However, the latter has no rims on the end margins. *Roundyella* also differs from *Egorovitina* in that the surface is covered with rather numerous thin spines, and in the adductor muscle-scar pattern.

The new genus resembles *Bideirella* Stover, 1956 (Middle Devonian of North America; Stover 1956, p. 1137, pl. 119, figs. 7–10; Moore 1961, p. 169, fig. 104. 1) still more, but *Bideirella* has a strongly pitted surface, acute ends in dorsal aspect and the vertical ridges near ends, which extend ‘. . . the full height of the valve’ and have no knobs, are not similar to the rims of *Egorovitina*.

There is also a certain similarity with *Parenthatia* Kay, 1940 (middle Ordovician of North America; Kay 1940, p. 359, pl. 32, figs. 43–46; Moore 1961, p. 129, fig. 62. 10, 11). The distinctions are in differently rounded extremities in *Parenthatia* and presence of a shallow transverse depression; besides that the marginal elevations, which resemble the ridge-like swellings of *Egorovitina*, are acuminate and crest-like in form.

As compared to *Moorites* Coryell and Billings, 1932, which has somewhat similar outline and rims on its ends, the new genus differs in the following characteristics: (1) both ends are evenly rounded; in *Moorites* the anterior is obliquely rounded (Coryell and Billings 1932, pl. 18, figs. 5–7; Bushmina 1968, pl. 6, figs. 1–8, 14); (2) cardinal angles indistinct; in *Moorites* they are clearly expressed (ibid.); (3) ventral margin straight; in *Moorites* it is often concave (ibid.); (4) surface with shallow, rather evenly distributed pits; in *Moorites* there are coarse pits, situated in elongate depressions between rims (Coryell and Billings 1932; Sohn in Moore 1961, fig. 115. 3a, 3e), or furrows (Bushmina 1968, pl. 6, figs. 5–8); (5) hinge adont with a groove on the left valve; in *Moorites* there are vertical teeth and sockets (Sohn in Moore 1961, fig. 115. 3d). The adductor muscle-scar patterns differ sharply. Scott gave the first description and schematic illustration of *Moorites* adductor muscle scar (Scott 1944, p. 171, fig. 22). The structure comprises three rounded spots, two at top, and one at base. It should be noted that Scott had in his possession moulds and it is not certain that the described adductor muscle scar belongs to *Moorites*, and not to *Youngiella* Jones and Kirkby, 1895. Scott’s figure is mentioned as *M. minutus* (Warthin) in the plate description, but in the text (p. 171) it is referred to as *M. convergens* (Bradfield), a species, which has been questionably referred by Bradfield (1935, p. 72, pl. 4, fig. 16) to *Youngiella*. The validity of *Moorites* has been called in question by some authors (Wilson 1933; Posner 1951) who believed it to

be a younger synonym of *Youngiella*. In any case the propinquity of both genera is indubitable and it is reasonable to consider the adductor muscle scar described by Scott as characteristic for the family Youngiellidae Kellet, 1933. A micrograph of the adductor muscle scar of *Y. naviculata* Posner, 1951, obtained by me, confirms Scott's data; the pattern consists of three round spots adjacent to each other.

Egorovitina differs also from *Moorites* and *Youngiella* in the free margin structure. According to my observations *Youngiella* possesses a calcified inner lamella and radial pore canals. It is noteworthy that Bradfield (1935, pp. 70, 74) mentioned that representatives of Youngiellidae may really belong with the Cytheridae; and Posner (1951, p. 71) indicated the presence of a pore-canal zone. In *Egorovitina* radial pore canals not observed.

The above facts show that *Egorovitina* gen. nov. and *Moorites* are distinct and should be classified into quite different families.

Egorovitina kirssanovi sp. nov.

Plate 52, figs. 1-16

Derivation of name. In honour of Mr. V. K. Kirssanov.

Type material. Holotype: Carapace, 1126/12-2. Paratypes: Four complete carapaces (1116/125, 1116/144-1, 1116/159, 1116/144-2), twelve left valves (1126/1-1, 2, 1126/2-1, 1126/3-1, 2, 3, 1126/8-2, 1126/9-1, 2, 1126/10-2, 4, 1126/26), and eight right valves (1126/1-4, 1126/2-2, 1126/7-2, 1126/8-1, 1126/9-3, 1126/10-1, 3, 1126/13-1). All types are from Viséan Stage (Alexinsky horizon), Borovitchi district, Novgorod, U.S.S.R.

Other material. Four carapaces and over twenty-five valves.

Diagnosis. Carapace small, in form close to a rectangular parallelepiped. The left valve is the larger. Extremities broadly rounded; the anterior is lower. Surface with shallow pits. Along both extremities ridge-like swellings with diagonal and oppositely placed elongate knobs present. Internal feature as for the genus and family.

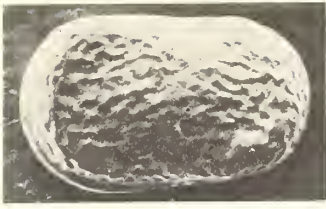
Description. Carapace small, up to 560 μ m, thin-walled, in form close to a rectangular parallelepiped. Left valve slightly overlaps right valve along the entire free margin. In dorsal view with equally truncated ends, and nearly parallel sides. Venter flattened.

In lateral view subrectangular, anterior and posterior margins evenly and broadly rounded; the former is lower. Dorsal margin straight, merging with anterior and

EXPLANATION OF PLATE 52

Figs. 1-16. *Egorovitina kirssanovi* sp. nov. Lower Carboniferous, Viséan, Alexinsky horizon, Borovitchi district, Novgorod region, U.S.S.R. 1-3, holotype, carapace, 1126/12-2. 1, right view, $\times 74$; 2, dorsal oblique, left side, $\times 72$; 3, dorsal, $\times 74$. 4, right valve, 1126/13-1, external view, $\times 78$. 5, left valve, 1126/26, internal view, $\times 76$. 6, right valve, 1126/10-1, adductor muscle scar, external view, $\times 150$. 7, 11, left valve, 1126/10-2. 7, external view, $\times 150$; 11, adductor muscle scar, external view, $\times 460$. 8, 15, left valve, 1126/1-1. 8, internal view, $\times 150$; 15, adductor muscle scar, internal view, $\times 460$. 9, 16, right valve, 1116/124. 9, external view, $\times 85$; 16, adductor muscle scar, internal view, $\times 460$. 10, right valve, 1126/9-3, adductor muscle scar, external view, $\times 460$. 12, left valve, 1126/9-2, adductor muscle scar, external view, $\times 460$. 13, left valve, 1126/1-2, adductor muscle scar, internal view, $\times 460$. 14, left valve, 1126/3-3, adductor muscle scar, external view, $\times 460$.

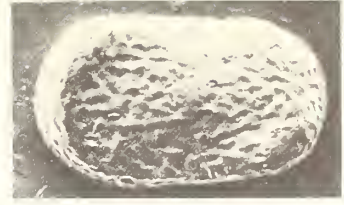
Figs. 1-5. Scanning electron micrographs (Cambridge Instruments 'Stereoscan 600', Al coating); figs. 6-16 transmitted light.



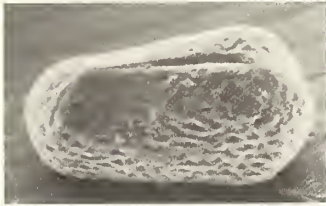
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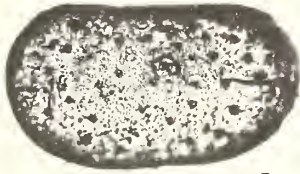
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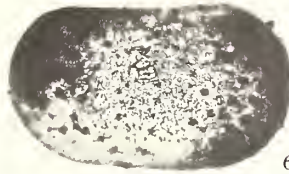
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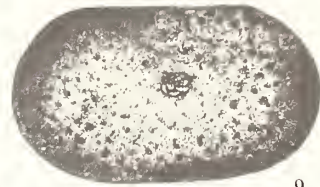
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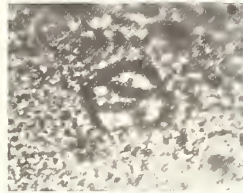
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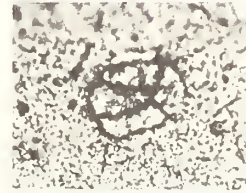
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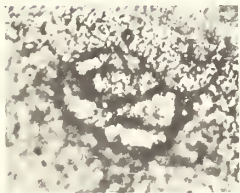
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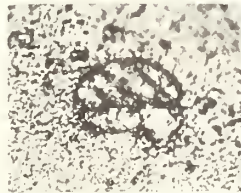
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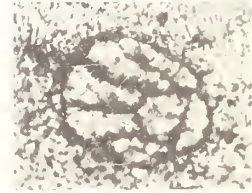
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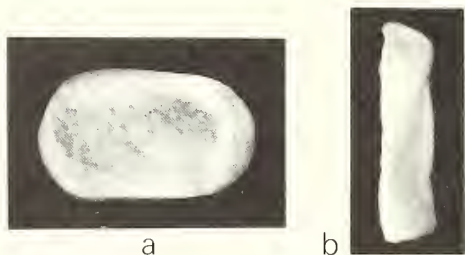


16

GRAMM, *Egorovitina kirssanovi* sp. nov.

posterior margins via obtuse cardinal angles. Ventral margin nearly parallel to dorsal and fluently curving merges with the ends.

Surface uniformly covered with shallow, smooth, and barely discernible pits. Fairly broad ridge-like swellings (rims) present along both extremities, limited



TEXT-FIG. 2. *Egorovitina kirssanovi* sp. nov. Right valve, 1116/124: a, external view; b, dorsal view, $\times 60$. Reflected light photographs. Lower Carboniferous, Viséan, Alexinsky horizon; Borovitchi district, Novgorod region, U.S.S.R.

proximally by gentle crescentic depressions. On right valve, at anterior cardinal angle, the swelling is weakly expressed; gradually becoming stronger and acquiring a rim-like form it reaches maximum in the antero-ventral part, where it forms a prominent elongate knob. On the posterior margin the rim is clearly distinguishable and reaches a maximum at the postero-dorsal cardinal angle as a prominent elongate knob. On the left valve the rims are developed more evenly and the maxima (elongated knobs), situated in antero-dorsal and postero-ventral parts, are not so strongly expressed. Owing to diagonal and oppositely placed elongate knobs,

the carapace in dorsal or ventral views has an obliquely compressed appearance.

Hinge adont; hinge-margin straight, thin with a narrow groove in the left valve.

Calcified inner lamella thin, narrow, and of uniform width, with a contact groove on the left valve. Walls are pierced with numerous, very thin normal pore canals; the distance between canals 2–3 μm , diameter less than 1 μm .

The adductor muscle scar, roughly circular in form, is located in the mid-valve or slightly in front and higher. Internally it is situated on a round feebly expressed elevation. The structure is compact, round, resembling a five-toed footprint. In the posterior or postero-ventral part there is a supporting spot, away from which five elongate spots are arranged in a pedate pattern. The uppermost is thin, elongate; the three middle spots are the longest, well developed, and spatulate anteriorly; the lowermost spot is usually short and relatively thick. In juvenile forms the upper and lower spots are often indistinct.

Mandibular and frontal spots not observed.

		Length (μm)	Height (μm)	Width (μm)
Carapace holotype	1126/12-2	525	310	225
Left valve	1126/3-1	235	150	—
Right valve	1126/2-2	275	170	—
Right valve	1126/10-1	275	160	—
Right valve	1126/9-3	275	—	—
Left valve	1126/3-2	280	170	—
Left valve	1126/2-1	285	170	—
Left valve	1126/10-2	285	170	—
Left valve	1126/9-2	325	200	—
Right valve	1126/1-4	325	—	—
Right valve	1126/10-3	330	200	—
Left valve	1126/10-4	330	200	—

		Length (μm)	Height (μm)	Width (μm)
Left valve	1126/1-2	360	210	75
Right valve	1126/7-2	385	225	90
Left valve	1126/3-3	385	225	—
Left valve	1126/8-2	390	225	100
Left valve	1126/1-1	400	230	90
Left valve	1126/9-1	400	240	—
Right valve	1116/124	475	275	105
Right valve	1126/8-1	475	275	110
Right valve	1126/13-1	500	290	—
Left valve	1126/26	500	300	—
Carapace	1116/159	550	315	250
Carapace	1116/125	550	325	225
Carapace	1116/144-1	550	325	250
Carapace	1116/144-2	560	330	205

Ontogeny. In smallest specimens, 235–285 μm long, the anterior is higher than the posterior and the dorsal margin is slightly concave (Pl. 52, figs. 6, 7); the adductor muscle scar is slightly posterior of mid-valve length. In specimens 325–475 μm long both extremities are of equal height, dorsal margin straight, adductor muscle scar located in the middle of the valve. In carapaces 550–560 μm long the posterior extremity becomes the highest and the adductor pattern is slightly anterior of mid-valve length. Thus during the ontogeny the interrelation of the height of the anterior or posterior ends and the position of adductor pattern changes.

The adductor muscle scar undergoes the following changes: the smallest specimen studied (235 μm long) has the supporting spot and three anterior spots; this leads to a suggestion that these four spots appear first; the upper and the lower spots emerge later. During the ontogeny an increase in the adductor pattern and separate spots took place, the anterior spots (especially the middle ones) grew and lengthened most.

Variability. The ridge-like swellings are differently expressed on different specimens. The adductor pattern is also variable; this is seen on the illustrations and finds expression in the length and shape of separate spots. On the young growth-stages the number and shape of spots is also variable (Pl. 52, figs. 10–12). Notable are an adductor pattern with differently placed anterior spots (Pl. 52, fig. 14) and a pattern with an irregular posterior supporting spot (Pl. 52, fig. 13); apparently they are pathological phenomena.

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